

***Cherax snowden*, a new species of crayfish (Crustacea, Decapoda, Parastacidae) from the Kepala Burung (Vogelkop) Peninsula in Irian Jaya (West Papua), Indonesia**

Christian Lukhaup¹, Jörn Panteleit², Anne Schrimpf²

1 Waldstrasse 5a, 66999 Hinterweidenthal, Germany **2** Conservation Genetics, Institute for Environmental Sciences, University Koblenz-Landau, Fortstrasse 7, 76829 Landau, Germany

Corresponding author: *Christian Lukhaup* (craykeeper@gmx.de)

Academic editor: *S. De Grave* | Received 17 July 2015 | Accepted 24 August 2015 | Published 24 August 2015

<http://zoobank.org/9D5A89C5-168B-4E1C-93B1-D3F00498D23B>

Citation: Lukhaup C, Panteleit J, Schrimpf A (2015) *Cherax snowden*, a new species of crayfish (Crustacea, Decapoda, Parastacidae) from the Kepala Burung (Vogelkop) Peninsula in Irian Jaya (West Papua), Indonesia. ZooKeys 518: 1–14. doi: 10.3897/zookeys.518.6127

Abstract

A new species, *Cherax snowden* **sp. n.**, from the Oinsok River Drainage, Sawiat District in the central part of the Kepala Burung (Vogelkop) Peninsula, West Papua, Indonesia, is described, figured and compared with the closest related species, *Cherax holthuisi* Lukhaup & Pekny, 2006. This species is collected and exported for ornamental purposes and its commercial name in the pet trade is “orange tip” or “green orange tip”. Both species may be easily distinguished morphologically or by using sequence divergence, which is substantial, for considering *C. snowden* **sp. n.** to be a new species.

Keywords

Crustacea, Decapoda, Parastacidae, *Cherax snowden* new species, freshwater crayfish, Oinsok River Drainage, Kepala Burung (Vogelkop) Peninsula, Irian Jaya, Indonesia, West Papua, pet trade

Introduction

The crayfish of the island of New Guinea were extensively studied by Holthuis (1949, 1956, 1958, 1982, 1986, 1996), with additions by Lukhaup and Pekny (2006, 2008a), Lukhaup and Herbert (2008), Lukhaup (2015), and Patoka et al. (2015). Nevertheless, over the last decade, there has been an increasing number of colourful crayfish, presumed to be a further undescribed species, sold from New Guinea in the ornamental fish trade in Europe and Asia under the names *Cherax* “orange tip”, and “green orange tip” (Lukhaup and Pekny 2008b, 2014). These have been exported to some countries in Europe, East Asia and America. Among the most common and popular colour forms are: (1) green, orange and yellow morph with orange tips (Fig. 1A–B); and (2) a greenish orange morph (Fig. 1C). While they are clearly species of *Cherax*, a large genus of freshwater crayfish occurring in Indonesia (West Papua), Papua New Guinea and Australia, their exact provenances could not be ascertained, with dealers claiming they came from Ajamaru (West Papua) and other places in the area that could not be confirmed. In the present contribution, this species is described as new to science and it is established that it is in fact native to the Oinsok River Drainage, Sawiat District of the Kepala Burung (Vogelkop) Peninsula, West Papua, Indonesia. The new species, *Cherax snowden*, differs from all other crayfish of this genus in the shape of its rostrum, shape of body and chelae and also in its colouration. *Cherax snowden* sp. n. is genetically and morphologically most similar to *Cherax holthuisi*, collected from the Kais River Drainage and Aitinjo Lake, Irian Jaya, Indonesia (Lukhaup and Pekny 2006).

These species may easily be distinguished on the basis of sequence divergence or by their colour and colouration pattern.

Material and methods

The first specimens of the new species were exported from the city of Sorong, Indonesia as *Cherax* sp. in 2006. Those crayfish have been captured by a unknown local collector from Kepala Burung for ornamental purposes in West Papua, Indonesia and imported to Aquarium Dietzenbach /Germany through Maju Aquarium / Jakarta . Several animals from the first import were photographed and then preserved in 70% ethanol. Due to their colouration the first author named them *Cherax* sp. “orange tip” and “green orange tip”. In April 2015 we received another 6 animals through Garnelio, a leading german online store specialized in freshwater invertebrates from Mannheim, Germany. Furthermore, we recieved 20 additional specimens from Aquazone Indonesia a wholesaler for freshwater fish and freshwater invertebrates through Garnelio. The name of the crayfish collector in Sawiat District collecting for Aquazone Indonesia and other wholesaler in Indonesia is Irianto

Wahid. According to the information obtained from Maju Aquarium and Aqua-zone Indonesia as well as from Irianto Wahid all specimens originated from creeks in the Sungai River Drainage. Two of the six animals obtained from Garnelio were photographed. All of them have been kept alive separately in aquarium tanks until samples of haemolymph were obtained for DNA analysis. After this procedure, the specimens were compared to the animals imported in 2006. They matched perfectly. They were subsequently preserved in 80% ethanol. One male from the shipment of April 2015 was selected as holotype, one female from the same shipment as allotype, another male as paratype.

DNA was extracted from muscle tissue using a standardized protocol ('High Salt DNA Extraction Protocol for removable samples'; Alijanabi and Martinez 1997). A 600 base pair (bp) long fragment of cytochrome c oxidase subunit I (COI) of mitochondrial DNA, was amplified using the primer pair LCO1490 (5'-ggccaacaatcataaagatattgg-3') and HCO2198 (5'-taaacttcagggtgacaaaatca-3') (Folmer et al. 1994). The polymerase chain reactions (PCR) were performed in a total volume of 20 µl, containing 0.125 µl GoTaq DNA Polymerase (Promega, Mannheim, Germany), 4 µl 5x Colorless GoTaq Flexi Buffer (Promega, Mannheim, Germany), 1.2 µl of 25 mM MgCl₂ (Promega, Mannheim, Germany), 0.4 µl of 25 mM/l dNTPs (Fermentas, St. Leon-Rot, Germany), 0.8 µl of both primers with a concentration of 10 pmol/µl and 2 µl of the sample DNA. The following PCR-program was used: 4 min at 94 °C followed by 30 cycles each with 45 s at 94 °C, 45 s at 47 °C and 1 min at 72 °C. The final extension time was 10 min at 72 °C. Afterwards, the PCR-products were stored at 8 °C. PCR products were sequenced on a 3730 DNA Analyzer eight capillary sequencer (Applied Biosystems, MA, USA) by the company SeqIT (Kaiserslautern, Germany). Sequences were edited with Geneious 7.1.7 software (Biomatters Ltd.). The sequence will be submitted to GenBank after acceptance of the manuscript.

Additional we have downloaded the following sequences from GenBank: HG942364 – *Cherax (Astaconephrops) quadricarinatus* (von Martens, 1868), KJ950502 – *Cherax bicarinatus* (Gray, 1845), KJ950510 – *Cherax communis* Holthuis, 1949, KJ950520 – *Cherax holthuisi*, KJ950526 – *Cherax murido* Holthuis, 1949, KJ950529 – *Cherax paniaicus* Holthuis, 1949, KJ950533 – *Cherax peknyi* Lukhaup & Herbert, 2008, KJ950507 – *Cherax (Astaconephrops) boesemani* Lukhaup & Pekny, 2008, KM501043 – *Cherax* sp. and as an outgroup we used NC_026214.1 – *Euastacus spinifer* (Heller, 1865) and HG799087 – *Cherax destructor* Clark, 1936. All sequences were aligned with Geneious. We used jModelTest (Darriba et al. 2012) to estimate the best nucleotide substitution model and the HKY+G model was selected by Bayesian information criterion (BIC). Phylogenetic relationships were reconstructed using MrBayes 3.2.1 (Ronquist and Huelsenbeck 2003) as implemented in Geneious. We ran four independent chains of 10 million generations with a subsample frequency of one thousand after a burn-in period of 1 million.

Systematics

Family Parastacidae Huxley, 1879

Genus *Cherax* Erichson, 1846

Cherax snowden sp. n.

<http://zoobank.org/136302EA-EEEE-4815-A5C3-6E37F29442A0>

Figs 1–5

Type material. Holotype: male (TL 96 mm) (MZB Cru 4291), Oinsok River Drainage, Sawiat District, Kepala Burung (Vogelkop) Peninsula, West Papua, Indonesia, collected by Irianto Wahid on 14 January 2015, exported through Aquazone Aquarium, Jakarta, Indonesia. Paratype: 1 male (TL 101 mm) (MZB Cru 4292), 1 allotype female (TL 77 mm) (MZB Cru 4293), same data as holotype.

Non-type material. 3 males (TL 69–84 mm) (MZB Cru 4294), same data as holotype.

Description of male holotype (Figs 2–5). Body and eyes pigmented. Eyes not reduced.

Body subovate, slightly compressed laterally. Pleon narrower than cephalothorax (width 18 mm and 20 mm respectively). Rostrum (Fig. 3A) slender, reaching about to end of ultimate antennular peduncle and one third as long as wide (width 6 mm at base, length 9 mm). Upper surface smooth, pitted, few scattered setae present at tip of rostrum; lateral margins of rostrum almost straight in basal part, distally rather moderately tapering towards apex. Margins slightly elevated continuing in rostral carinae on carapax. Lateral rostral margins bearing each 2 blunt spines in distal third, few short hairs present on base of rostral margins, punctated at base. Rostral carinae extending as slight elevation posteriorly on carapace, fading shortly after beginning of postorbital ridges. Postorbital ridges well developed terminating in slightly upturned corneous spines anteriorly, fading posteriorly at two-thirds of occipital carapace length. Dorsal surface of carapace smooth, pitted, cervical and branchiocardiac grooves distinct, non-setose. Short setae present on caudal margin. Areola length 17 mm narrowest width 6 mm. Length of areola 36.95% of total length of carapace (46 mm).

Ventrolateral parts smooth with scattered pitted; anterior margin strongly produced, rounded upper margin directed inward. Dorsal surface of pleon smooth, with scattered pits; abdominal segments with short setae present on caudal margins.

Eyes rather large; cornea globular, darkly pigmented, about as long as eyestalk; eyestalk slightly narrower than cornea.

Antennulae and antennae typical for the genus. Antennae about as long as body. Antennular peduncle reaching slightly beyond acumen, antennal peduncle reaching slightly beyond apex of scaphocerite. Scaphocerite (Fig. 3B) broadest at midlength, convex in distal part becoming narrower in basal part; thickened lateral margin terminating in large corneous spine, almost reaching distal margin of ultimate segment of antennular peduncle. Right scaphocerite 8 mm long and 3.5 mm wide. Proximal margins setose. Coxicerite of antennal peduncle with spinuous tubercle anteriorly; basicerite with one lateral and one ventral spine and hooked tubercles.



Figure 1. *Cherax snowden* sp. n. **A** paratype male (MZB Cru 4292) from Oinsok River drainage, Sawiat District **B** male from aquarium import (not listed in material examined) from Indonesia **C** Paratype female (MZB Cru 4293) from a unnamed tributary of the Oinsok River drainage.



Figure 2. *Cherax snowden* sp. n. holotype male (MZB Cru 4291).

Epistome broadly triangular becoming lance-shaped, with corneous spine at anterior tip, lateral surface with small tubercles; central surface smooth, excavate. Mouth-parts typical for the genus.

First pereopods equal in form, chelae not gaping. subequal in size, left cheliped largest (48 mm long, 18 mm wide, 10 mm high), probably replaced. Right chelae (Fig. 3C–D) 46 mm long, 20 mm wide, 11 mm high) strongly compressed. Fingers shorter than palm (dactylus 19 mm long). Dactylus broad at base, tapering slightly towards tip, becoming about 1/2 as broad as at base. Tip with sharp, corneous, hooked tooth pointing outwards at an angle of 45°. Cutting edge of dactyl with a continuous row of rather small granular teeth and one prominent larger tooth at about middle of cutting edge. Ventral and dorsal surface of movable finger with scattered punctuation. three rows of short setae present at posterior half of the cutting edge. Fixed finger triangular, merging gradually into palm, ending in sharp, corneous, hooked tooth, standing almost perpendicular to axis of finger. Upper surface of palm practically smooth, slightly pitted, more densely pitted at margins. Five rows of short setae present in posterior part. Mesial margin of palm with a row of 23–24 tubercles. Dorsal surface of carpus (14 mm) smooth and pitted, with slight excavation in middle part. Ventral carpal surface margins slightly elevated; inner margin with set of 6–7 small granules and one acute spiniform tubercle oriented in an angle of approx 45°.

Merus (23 mm) laterally depressed in basal part; surface smooth and pitted; row of 6–7 tubercles present and a prominent spine at anterior part. Dorsolateral margin with one corneous tubercle; row of small granules on entire inner ventrolateral margin with

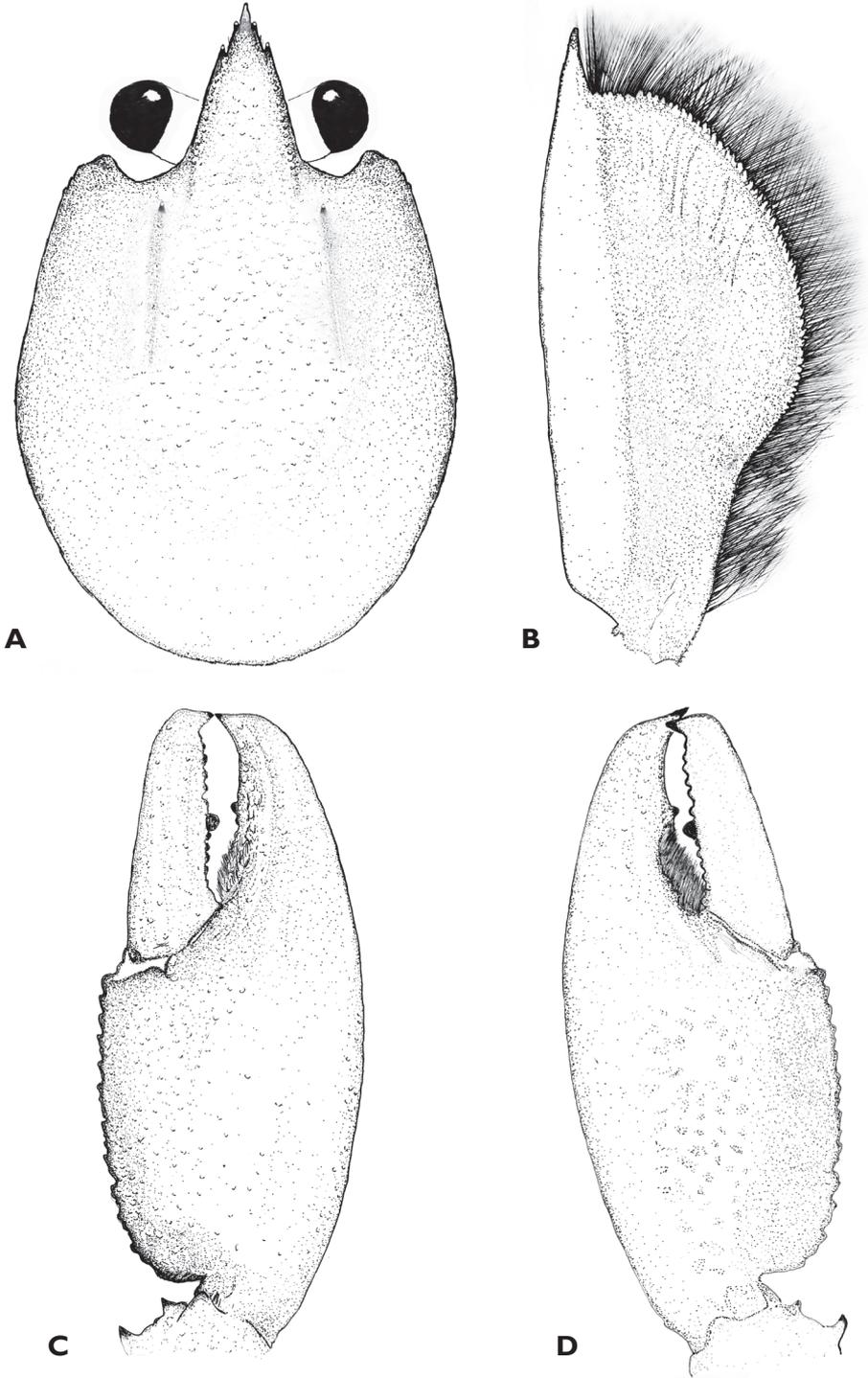


Figure 3. *Cherax snowden* sp. n. holotype male (MZB Cru 4291) **A** dorsal view carapace **B** scaphocerite **C** dorsal view right chela **D** ventral view left chela.



Figure 4. *Cherax snowden* sp. n. holotype male (MZB Cru 4291) dorsal view of cephalothorax.

3 prominent spines at the anterior part. Ischium (12 mm) smooth with single granule on ventral surface.

Second pereopod reaching about to apex of scaphocerite. Finger as long as palm, of same height. Short setae present on dactyl and fixed finger, getting more dense anteriorly. Cutting edge of fixed finger and carpus with row of short setae. Carpus slightly longer than palm. Merus (15 mm) about 1.7 times longer than carpus (9 mm). Ischium (7 mm) about half as long as merus.

Third pereopod overreaching second. Fingers shorter than palm.

Fourth pereopod reaching distal margin of scaphocerite. Dactylus with corneous tip. Short setae present. Propodus more than twice as long as dactylus, about 1.5 times as long as carpus; somewhat flattened, carrying stiff setae on lower margin. Merus just slightly longer than propodus.

Fifth pereopod similar to fourth, slightly shorter.

Dorsal surface of pleon smooth in median region; pleura smooth, slightly pitted, becoming densely pitted on sixth somite and telson. Telson with posterolateral spines, dense short setae present in the posterior third. Posterior margins setose. Uropodal protopod with distal spine on mesial lobe. Exopod of uropod with two well defined spines. One distal spine on mesial lobe, with prominent median rib ending in a spine in middle of uropod. Posterior margin of proximal segment of exopod of uropod with row of small spines overlapping diarsis. Short setae present on posterior third of dorsal surface of endopod and exopod. Ventral surface of telson, endopod and exopod smooth, not pitted. Margines of exopod setose.



Figure 5. *Cherax snowden* sp. n. holotype male (MZB Cru 4291) **A** left first chela, ventral aspect **B** right first chela, dorsal aspect.

Description of paratype female (Fig. 6). Chela of first pereiopods equal, about 2 times as long as broad (24 mm and 11 mm respectively). Mesial margin of palm slightly elevated, forming slender serrated ridge with row of 13–14 small granular teeth. Cutting edge of dactyl with rather small granular teeth in posterior part and one slightly larger tooth in about middle. Cutting edge of fixed finger with small granules and one slightly larger granules. Small scattered short setae visible along ventral cutting edge of chelae, more dense in posterior area. Cervical groove distinct, non setose. Cephalothorax just slightly narrower than pleon (widths 14 mm and 16 mm respectively).

Size. The males examined have a carapace length of 31–43 mm, and a total length of 69–101 mm ($n = 5$); the female has a carapace length of 34 mm and a total length of 77 mm ($n = 1$).

Colouration. The living animals (Fig. 1A–C) are coloured as follows. Chelae dark green to light green or greenish gray, distal part of the lower margin cream to orange. Tips of chelae orange.

Cephalothorax dark green, light green, brown green, sometimes blueish green fading ventrally to cream, beige or orange. Pleon same colour as cephalothorax with transverse orange bands, pleura creamy to orange with a black, brown or dark green band. Walking legs from dark green to blueish gray or creamy yellow, sometimes brown yellow. Distal margin of tail-fan cream to orange.

Systematic position. *Cherax snowden* sp. n. differs from *C. holthuisi* in the shape of the rostrum, number of rostral teeth, the shape of the chelae and coloration. While



Figure 6. *Cherax snowden* sp. n., paratype female (MZB Cru 4293).

C. holthuisi has just two indentations on each side in the distal part of the rostrum and no spines present, *Cherax snowden* sp. n. has 2 rostral teeth on each side near the apex. *Cherax holthuisi* usually is orange to pale, creamy or light brown, rarerly light blue, while the new species is dark green to light green or greenish gray. Tips of the chelae in the new species are striking orange. Eyes in *C. holthuisi* rather small compared to the eyes of *C. snowden* sp. n.

The phylogenetic tree revealed that *C. snowden* sp. n. forms a strong supported clade with an undescribed *Cherax* sp. individual that was collected in Sorong West Papua, Indonesia (GenBank accession number: KM501043). The two sequences in this clade differ by only 9 base pair substitutions (1.5%). The low genetic divergence of the undescribed *Cherax* sp. and the close geographic sampling origin indicate that this individual is the same species as the here new described species. The *C. snowden* sp. n. and *Cherax* sp. clade group next to the clade which includes *Cherax* sp. nov. A and *C. holthuisi*. The species of these two neighbouring clades differ by 9.2% (*Cherax* sp. to *Cherax* sp. nov. A) to 9.7% (*C. snowden* sp. n. to *C. holthuisi*), respectively. The strong genetic divergence of *C. snowden* sp. n. to the next related described *Cherax* species indicates that *C. snowden* sp. n. is indeed a new species.

Holthuis (1949) in his publication on the New Guinea *Cherax* considered species should be placed into two groups. One with the rostral and median carine absent or weakly developed and referred to as the *Cherax* group following the characteristics of the type species, *C. preissii* (Erichson, 1846) from southwest Australia. The other group contains species that have rostral and sometimes the median carina well developed and referred to as the *Astaconephrops* group with Nobili's (1899) *Astaconephrops albertisii* as the type. Newly described species have been placed into one or other of the two subgenera (Lukhaup and Pekny 2006, 2008; Lukhaup and Herbert 2008; Lukhaup 2015; Patoka et al. 2015). Munasinghe et al. (2004b) and Austin (1996) and Austin and Knott (1996) however identified three geographically-based lineages within *Cherax* based on molecular phylogenetic studies: a southwestern group, an eastern group and a northern group. Support for the latter group however was based on only very limited sampling

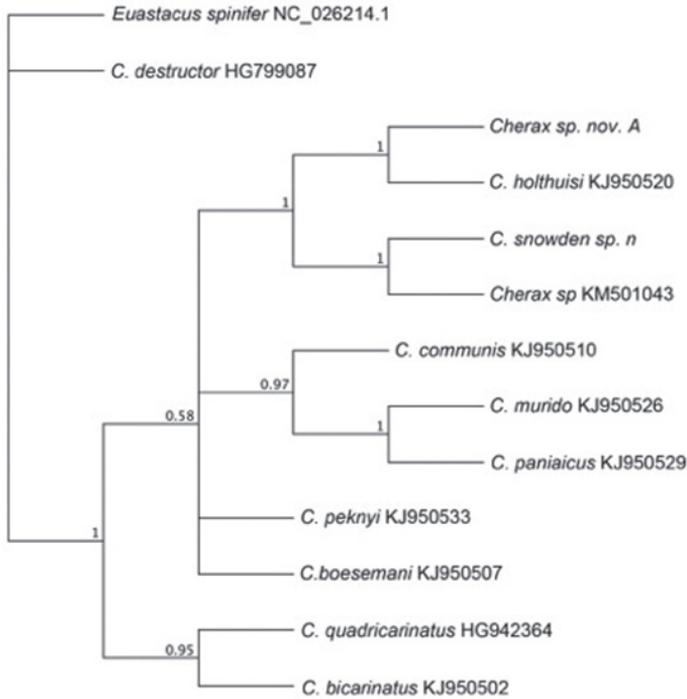


Figure 7. Phylogenetic consensus tree inferred from a 600 bp long fragment of COI with MrBayes. Shown are posterior probability values.

(e.g. single samples of *C. quadricarinatus*, *C. rhynchotus* Riek, 1951 and *C. peknyi* in Munasinghe et al.'s study) (Munasinghe et al. 2004b) indicate that the division of *Cherax* into two subgenera, as conceived by Holthuis and subsequent authors dealing with New Guinea crayfish has to be reconsidered. Based on Munasinghe et al. (2004b) and Austin (1996) and Austin and Knott (1996) *Cherax snowden* sp. n. belongs to the northern species group lineage consisting of 21 species:

C. albertisii; *C. boesemani*; *C. boschmai* Holthuis, 1949; *C. buitendijkae* Holthuis, 1949; *C. communis*; *C. divergens* Holthuis, 1950; *C. gherardii* Patoka, Bláha & Kouba, 2015; *C. holthuisi*; *C. longipes* Holthuis, 1949; *C. lorentzi lorentzi* Roux, 1911; *C. lorentzi aruanus* Roux, 1911; *C. minor* Holthuis, 1996; *C. misolicus* Holthuis, 1949; *C. monticola* Holthuis, 1950; *C. murido* Holthuis, 1949; *C. pallidus* Holthuis, 1949; *C. paniaicus* Holthuis, 1949; *C. papuanus* Holthuis, 1949; *C. peknyi*; *Cherax pulcher* Lukhaup, 2015; *C. solus* Holthuis, 1949.

Etymology. The new species is named after the american freedom fighter Edward Joseph Snowden. He is honored due to of his extraordinary achievements in defense of justice, and freedom. The name is used as a noun in apposition.

Ecology. Known only from tributary creeks to the Oinsok River, Sawiat District in the central part of the Kepala Burung (Vogelkop) Peninsula. The creeks from where these crayfish have been collected are shallow (20–60 cm) with a moderate flow, the

water is clear, and has a pH of approx. 6.5. In most of the parts no water plants are present. The substrate of the creek is rocky, mostly covered with silt, stones and larger rocks. To improve the knowledge of the distribution of the species more collecting trips are necessary.

It is also necessary to briefly comment on the possible threats faced by the new species. As *C. snowden* sp. n. is collected in large numbers for the global aquarium trade, as well as for food for the growing local population, the crayfish population will invariably be adversely impacted. According to local collectors, the populations of the species have been decreasing in the last few years. Clearly, the continued collecting of these crayfish for the trade is not a sustainable practice, and if the popularity of the species continues, a conservation management plan will have to be developed, potentially including a captive breeding program.

Acknowledgements

Theresia Sutedja and Sum Sum Kintajaya (Aquazone, Indonesia) are thanked for the support finding the location of this interesting species. Farschad Farhadi and Garnelio are acknowledged for the crayfish they sponsored.

Dennerle is thanked for sponsoring parts of the trip to West Papua. Herbert Nigl (Aquarium Dietzenbach) provided valuable information and sponsored the species. Finally, Charles Fransen and Sammy De Grave are acknowledged for helpful comments. We thank Nikson Solossa and Marten Luter Salossa for information on the habitat.

References

- Ahyong ST (2014) Diversity and distribution of Australian freshwater crayfish with a check-list of the world Parastacidae and a key to the genera (Decapoda, Astacidea, Parastacoidea). *Advances in Freshwater Crustacean Systematics and Biology. Crustaceana Monographs* 19: 245–271.
- Aljanabi SM, Martinez I (1997) Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. *Nucleic acids research* 25(22): 4692–4693. doi: 10.1093/nar/25.22.4692
- Austin CM (1996) Systematics of the freshwater crayfish genus *Cherax* Erichson (Decapoda: Parastacidae) in northern and eastern Australia: electrophoretic and morphological variation. *Australian Journal of Zoology* 44: 259–296. doi: 10.1071/ZO9960259
- Austin CM, Knott B (1996) Systematics of the freshwater crayfish genus *Cherax* Erichson (Decapoda: Parastacidae) in south-western Australia: electrophoretic, morphological and habitat variation. *Australian Journal of Zoology* 44: 223–258. doi: 10.1071/ZO9960223
- Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9(8): 772.
- Erichson WF (1846) Übersicht der Arten der Gattung *Astacus*. *Archiv für Naturgeschichte* 12: 86–103, 375–377.

- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299.
- Holthuis LB (1949) Decapoda Macrura with a revision of the New Guinea Parastacidae. Zoological results of the Dutch New Guinea Expedition 1939. No. 3. *Nova Guinea* (n. ser.) 5: 289–330, pls. 2–9.
- Holthuis LB (1956) Native fisheries of freshwater Crustacea in Netherlands New Guinea. Contributions to New Guinea Carcinology. I. *Nova Guinea* (n. ser.) 7(2): 123–137, figs 1–3, pls. 1–8.
- Holthuis LB (1958) Freshwater Crayfish in Netherlands New Guinea Mountains. *South Pacific Commission Quarterly Bulletin* 8(2): 36–39, 7 figs.
- Holthuis LB (1982) Freshwater Crustacea Decapoda of New Guinea. In: Gressitt JL (Ed.) *Biogeography and ecology of New Guinea*, vol. 2. *Monographiae Biologicae* 42: 603–619, figs 1–5. doi: 10.1007/978-94-009-8632-9_28
- Holthuis LB (1986) The freshwater crayfish of New Guinea. *Freshwater Crayfish* 6: 48–58, figs 1–8.
- Holthuis LB (1996) *Cherax (Astaconephrops) minor* new species, a parastacid from the mountains of Irian Jaya (W. New Guinea) Indonesia (Crustacea: Decapoda: Parastacidae). *Zoologische Mededelingen Leiden* 70(24): 361–366, figs 1–2.
- Huxley TH (1879) *The Crayfish: an Introduction to the Study of Zoology*. C. Kegan Paul & Co., London.
- Lukhaup C (2015) *Cherax (Astaconephrops) pulcher*, a new species of freshwater crayfish (Crustacea, Decapoda, Parastacidae) from the Kepala Burung (Vogelkop) Peninsula, Irian Jaya (West Papua), Indonesia. *ZooKeys* 502: 1–10. doi: 10.3897/zookeys.502.9800
- Lukhaup C, Herbert B (2008) *Cherax peknyi* sp. nov., a new species of crayfish (Crustacea: Decapoda: Parastacidae) from the Fly River Drainage, Western Province, Papua New Guinea. *Memoirs of the Queensland Museum* 52(2): 213–219.
- Lukhaup C, Pekny R (2006) *Cherax holthuisi*, a new species of crayfish (Crustacea: Decapoda: Parastacidae) from the centre of the Vogelkop Peninsula in Irian Jaya (West New Guinea), Indonesia. *Zoologische Mededelingen Leiden* 80–1(7): 101–107, figs 1–4.
- Lukhaup C, Pekny R (2008a) *Cherax (Astaconephrops) boesemani*, a new species of crayfish (Crustacea: Decapoda: Parastacidae) from the centre of the Vogelkop Peninsula in Irian Jaya (West New Guinea), Indonesia. *Zoologische Mededelingen Leiden* 82(33): 331–340, figs 1–8.
- Lukhaup C, Pekny R (2008b) *Süßwasserkrebse aus aller Welt Gebundene Ausgabe*. Dähne Verlag, Ertlingen.
- Lukhaup C, Pekny R (2014) *Wirbellose - Garnelen, Krebse, Krabben & Schnecken im Süßwasseraquarium. Gebundene Ausgabe*. Dähne Verlag, Ertlingen, 300 pp.
- Munasinghe DHN, BurrIDGE CP, Austin CM (2004a) The systematics of freshwater crayfish of the genus *Cherax* Erichson (Decapoda: Parastacidae) in eastern Australia re-examined using nucleotide sequences from 12S rRNA and 16S rRNA genes. *Invertebrate Systematics* 18: 215–225. doi: 10.1071/IS03012
- Munasinghe DHN, BurrIDGE CP, Austin CM (2004b) Molecular phylogeny and zoogeography of the freshwater crayfish genus *Cherax* Erichson (Decapoda: Parastacidae) in

- Australia. *Biological Journal of the Linnean Society* 81: 553–563. doi: 10.1111/j.1095-8312.2003.00299.x
- Patoka J, Blaha M, Kouba A (2015) *Cherax (Astaconephrops) gherardii*, a new crayfish (Decapoda: Parastacidae) from West Papua, Indonesia. *Zootaxa* 3964(5): 526–536. doi: 10.11646/zootaxa.3964.5.2
- Ronquist F, Huelsenbeck JP (2003) MrBayes version 3.0: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19(12): 1572–1574. doi: 10.1093/bioinformatics/btg180

Redescriptions of *Nereis oligohalina* (Rioja, 1946) and *N. garwoodi* González-Escalante & Salazar-Vallejo, 2003 and description of *N. confusa* sp. n. (Annelida, Nereididae)

Víctor M. Conde-Vela¹, Sergio I. Salazar-Vallejo¹

¹ *El Colegio de la Frontera Sur, CONACYT, Departamento de Sistemática y Ecología Acuática, Chetumal, México*

Corresponding author: *Victor M. Conde-Vela* (victorconde2323@gmail.com)

Academic editor: *Chris Glasby* | Received 12 March 2015 | Accepted 9 August 2015 | Published 25 August 2015

<http://zoobank.org/4A0139A5-AE60-4988-ACFA-A16E8EEF35DB>

Citation: Conde-Vela VM, Salazar-Vallejo SI (2015) Redescriptions of *Nereis oligohalina* (Rioja, 1946) and *N. garwoodi* González-Escalante & Salazar-Vallejo, 2003 and description of *N. confusa* sp. n. (Annelida, Nereididae). ZooKeys 518: 15–49. doi: 10.3897/zookeys.518.9564

Abstract

Type material of several polychaete species described by Enrique Rioja from Mexican coasts are lost, and the current status of some species is doubtful. *Nereis oligohalina* (Rioja, 1946) was described from the Gulf of Mexico, but it has been considered a junior synonym of *N. occidentalis* Hartman, 1945, or regarded as a distinct species with an amphiamerican distribution. On the other hand, *N. garwoodi* González-Escalante & Salazar-Vallejo, 2003, described from Chetumal Bay, Caribbean coasts, could be confused with *N. oligohalina*. In order to clarify these uncertainties, *N. oligohalina* is redescribed based on specimens from the Mexican Gulf of Mexico, including a proposed neotype; further, *N. garwoodi* is redescribed including the selection of lectotype and paralectotypes, and *N. confusa* sp. n. is described with material from the Gulf of California. A key for the identification of similar species and some comments about speciation in nereidid polychaetes are also included.

Keywords

Amphiamerican, taxonomy, estuarine nereidids, cryptic species, Polychaeta

Introduction

Among the non-marine polychaetes, the family Nereididae de Blainville, 1818 has the largest number of brackish and freshwater species (61), and 31 out of these species occur in estuaries and coastal lagoons (Glasby et al. 2009). Of the 40 species of nereidid species recorded from the Gulf of Mexico (Fauchald and Solís-Weiss 2009), seven are reported in brackish or freshwater areas, and among the 10 species belonging to *Nereis*, only *N. oligohalina* (Rioja, 1946) is reported from estuaries (Glasby et al. 2009).

Enrique Rioja documented extensively the Mexican polychaetes from Pacific or Atlantic coasts in a series of papers; unfortunately, his material is lost, and most species require designation of neotypes (Salazar-Vallejo 1989). Rioja (1946) dealt with three estuarine nereidids from Veracruz, Mexico; he regarded one as a known species, *Neanthes succinea* (Leuckart, 1847), and the two others were described as new: *Neanthes oligohalina* and *Lycastopsis tecolutlensis*. The former species is now regarded as belonging in *Alitta*, but it differs from the North Sea species (T.F. Villalobos-Guerrero, pers. comm.); *L. tecolutlensis* was regarded as a junior synonym of *Namanereis amboinensis* (Pflugfelder, 1933), nowadays a widespread species (Glasby 1999); and *N. oligohalina* has been regarded as amphiamerican (Dean 2001), or restricted to Atlantic coasts (Santos and Lana 2003, Liñero-Arana and Díaz-Díaz 2007). However, other amphiamerican species have been shown to be restricted to one coast or the other, often resulting in description of new taxa (e.g. Carrera-Parra and Salazar-Vallejo 2011; Yáñez-Rivera and Carrera-Parra 2012). On the other hand, the Caribbean species *N. garwoodi* González-Escalante & Salazar-Vallejo, 2003 could be confused with *N. oligohalina*, and without an updated description of the latter, a synonymy can be anticipated.

However, *Nereis oligohalina* and *N. garwoodi* have morphological differences that separate them. In this contribution our objectives were first, to redescribe *N. oligohalina* based upon material collected from Veracruz, including topotypes, and to propose a neotype. Second, to redescribe *N. garwoodi* to clarify some doubtful features in the original description, and to select lectotype and paralectotypes specimens from the syntype series. Third, to recognize what has been regarded as *N. oligohalina* from the Mexican Pacific as a distinct species and describe it as *N. confusa* sp. n., based upon material from the Gulf of California. Further, a key to identify similar *Nereis* species and comments about species delimitation are also included.

Material and methods

Specimens studied are deposited in the Reference Collection of El Colegio de la Frontera Sur, Chetumal (ECOSUR) including ethanol-fixed specimens (ECOSUR-OH), and in the Polychaetological Collection of the Universidad Autónoma de Nuevo León (UANL).

Topotypes of *N. oligohalina* from Estero Casitas, Nautla were examined, including additional specimens that were recently collected along the coast of Veracruz, Mexico,

Gulf of Mexico. Specimens of *N. confusa* sp. n. from Bahía La Paz and Bahía de Los Ángeles, Gulf of California were found in unidentified material in ECOSUR, now formally deposited. To assess variation in paragnath morphology, specimens of *N. pelagica* Linnaeus from England (ECOSUR P2840), and *Pseudonereis* sp. from the Caribbean Sea (ECOSUR P1170), were also examined.

The best preserved specimens were used for designation of type material. Some specimens were fixed and preserved in 96% ethanol directly, otherwise the specimens were fixed with formalin and later preserved in 70% ethanol.

For analysis of variation, type materials and a number of non-type specimens for each species were measured. Total body length (TL), length up to chaetiger 3 (L_3) or 10 (L_{10}), width at same chaetigers (W_3 and W_{10}), number of chaetigers (nC), and length of longest tentacular cirrus (rTC) were measured with a millimeter rule under the stereomicroscope. TL was measured from palp tips to the end of the pygidium, W_3 and W_{10} were measured excluding parapodia. Also, paragnath numbers in all areas were counted; if the pharynx was not everted, a ventral dissection was made, and areas VII-VIII were described as if the pharynx was exposed. With these results simple descriptive statistics (mean, range and standard deviation) were performed. As different fixation methods were used, a Mann-Whitney U-test was used for evaluating if there were significant differences in body measures as a result of fixation method.

For the microscopical observation of parapodial features and chaetae, right-side parapodia along body were removed and mounted in semi-permanent slides; the photographs were made with a digital camera, and distal-view drawings of parapodia were included to depict spatial disposition of ligules and chaetae. Descriptions of pigmentation patterns were included, because they are consistent and useful for recognizing the three species; other authors have noted their utility for identifying cryptic nereidid species (Read 2007, Glasby et al. 2013).

Bakken and Wilson's (2005) terminology was followed for describing parapodia, and Bakken et al. (2009) for paragnaths. Parapodia from both atokes and epitokes (if available) were illustrated to show parapodial changes along the body. For determining dorsal cirri length and position of attachment, we considered the beginning of the dorsal or notopodial ligule to be approximately at the same vertical position of attachment as the ventral cirri; therefore, the relative length of dorsal cirrus was measured from that position toward the distal end of dorsal or notopodial ligule. The dorsal cirrus was considered basally attached if placed at, or near such a position, or medially attached if it was displaced more distally from that position.

Also, the reach of the dorsal cirrus and its relative length in respect of the dorsal or notopodial ligules were considered as separate attributes. For determining the reach of the dorsal cirrus, the tips of the both dorsal cirrus and dorsal or notopodial ligules were taken into account; if the dorsal cirrus tip extended beyond the tip of the dorsal or notopodial ligule, then we report "dorsal cirrus extended beyond dorsal/notopodial ligule" rather than "dorsal cirrus longer than dorsal/notopodial ligule". On the contrary, if dorsal cirrus is shorter or not exceeding the dorsal or notopodial ligules, then we report "dorsal cirrus not extended beyond dorsal/notopodial ligule". In the species

herein treated, length of dorsal cirri and length of dorsal or notopodial ligules were generally subequal, and the dorsal cirri change their attachment along the body, but not their length necessarily.

For the designation of lectotype and neotype, the International Code of Zoological Nomenclature (ICZN 1999) was followed. The designation of a neotype for *N. oligohalina* follows Article 75, and the designation of a lectotype for *N. garwoodi* follows Article 74 (ICZN 1999). The non-formal term ‘paraneotypes’ is used for figured topotypic specimens (Evenhuis 2008), and their utility has been pointed out elsewhere (Salazar-Vallejo 2011, Sendall and Salazar-Vallejo 2013).

Results

Family Nereididae de Blainville, 1818

Genus *Nereis* Linnaeus, 1758

Type species. *Nereis pelagica* Linnaeus, 1758, by subsequent designation (Hartman 1948:63).

Remarks. Linnaeus (1758:654) listed five species under *Nereis*: *N. lacustris* (now *Stylaria lacustris*, an oligochaete), *N. caerulea* (questionable after Hartman 1959:254), *N. gigantea* (after Hartman 1959:259, same as *Hermodice carunculata* (Pallas, 1766), rendering it a *nomen oblitum* because it would have priority over Pallas’ name), *N. pelagica*, and *N. noctiluca*. Further, it was Hartman (1948:63) who fixed the type species, and therefore this should be regarded as a subsequent designation (ICZN 1999, Art. 69.1), in contrast to Bakken and Wilson (2005) who regarded it as an original designation.

Although the species described here have more attributes than those included in the current diagnosis of the genus (Bakken and Wilson 2005), the generic diagnosis was not modified because it first requires a redescription of the type-species, and a phylogenetic analysis with subsequent delimitation of the genus. Among the traditionally used features for descriptions and delimitation of *Nereis* species are some that are highly variable, especially paragnath number. Bakken et al. (2009) made a useful revision of paragnath morphology and introduced new terminology to standardize descriptions. In addition to conical paragnaths, the species described here present other types of paragnaths that are not currently included in the diagnosis of the genus. Conical paragnaths are pointed to various degrees, being more acute in the maxillary ring, especially on area II. The pyramidal paragnaths in *N. oligohalina* and *N. garwoodi* have quadrilateral bases but they can also be polygonal, having more defined surfaces in the latter species. Further, *N. confusa* sp. n. apparently has smooth bars on area IV, but a closer inspection confirms that this is an artifact because the bars are formed by lateral and basal fusions of some small conical paragnaths (Fig. 6H); these modified structures were regarded as melted paragnaths (Bakken et al. 2009). However, Glasby et al. (2011) suggested limiting use of the term for conical paragnaths mounted on a plate-like basement as occurs in *Neanthes pachychaeta* (Fauvel, 1918), and Villalobos-Guer-

rero and Carrera-Parra (2015) found paragnaths on a soft basement in *A. acutifolia* (Ehlers, 1901). Because neither a basement is present in *N. confusa* sp. n., we suggest the term ‘merged’ for paragnaths fused at the base but without formation of a plate.

In his revision of *Pseudonereis* Kinberg, 1865, Bakken (2007) introduced the term ‘P-bar’, which was later defined by Bakken et al. (2009) as “small bars having a protruding apex in one end of the bar”; and they can appear in areas II, III, IV and VII–VIII, often accompanied by conical paragnaths. The monophyly of *Pseudonereis* was supported by, among other characters, the presence of both P-bars and paragnaths in comb-like rows (Bakken 2007). The *Nereis* species studied herein have two main rows, each one with other two sub-rows; the anterior-most sub-rows are often aligned horizontally, while the posterior-most ones form a jagged line. The anterior-most rows have P-bars alternating with conical or pyramidal paragnaths in a similar way as in *Pseudonereis* (Fig. 6D–F), which has been also reported for *Alitta* (Villalobos-Guerrero and Carrera-Parra 2015). Therefore, P-bars are not an exclusive feature of *Pseudonereis* as Bakken et al. (2009) concluded.

The neuropodial postchaetal lobe has been considered absent for *Nereis* species in recent phylogenetic analyses (Bakken and Wilson 2005, Santos et al. 2005). Nevertheless some authors indicate its presence; Read (1980) for *N. ovariatus* (Read), Santos and Lana (2003) for *N. pseudomoniliformis* (Santos and Lana), Chambers and Garwood (1992) for *N. pelagica* (and corroborated by us), and Darbyshire (2014) for *N. eugeniae* (Kinberg, 1865). Also, the three species herein described have postchaetal lobes shorter or subequal than neuroacicular ligules, and in epitoke specimens these lobes carry natatory lamellae; therefore, we considered postchaetal lobes as present in *Nereis*.

Reproductive nereidids or epitokes can have two or three different regions; parapodial cirri and the pygidium are transformed is especially relevant for chemoreception, parapodial lobes or ligules are expanded and chaetae replaced for swimming (Herpin 1925, Boilly-Marer 1972). Charrier (1920) studied muscular tissue transformation associated with epitoky in the commensal species *Nereis fucata* (Savigny in Lamarck, 1818) (currently belonging to *Neanthes* Kinberg). He observed that parapodial cirri vary in some features as the length relative to corresponding ligules, the modifications of attachment and the displacement along the body; in fact, the attachment site of dorsal cirrus often show a distal displacement along notopodial ligules.

***Nereis oligohalina* (Rioja, 1946)**

Figures 1, 2, 6A, D, J–L, O, Q

Neanthes oligohalina Rioja 1946: 207–210, pl. 1, figs 3–6, pl. 2, figs 13–19; 1947: 529, 531; 1960: 295.

Nereis oligohalina Hartman 1951: 46; 1954: 414.

Type material. Veracruz, Mexico. Neotype ECOSUR 0172 and paraneotypes ECOSUR 0173 (5), mouth of Actopan River (19°25'2.95"N, 96°19'32.28"W), Chacha-

lacas Sandbar, Gulf of Mexico, 1 m depth, on *Crassostrea virginica* reef, fine sediment, April 10 2012, Coll. V.M. Conde-Vela, A.E. Te-Gómez.

Additional material. Veracruz, Mexico. ECOSUR P2826 (15), and ECOSUR P2827 (37), Mouth of Actopan River (19°25'2.95"N, 96°19'32.28"W), Chachalacas Sandbar, Gulf of Mexico, 1 m depth, on *Crassostrea virginica* reef, fine sediment, April 10 2012, Coll. C. Licona-Rosado, V.M. Conde-Vela, A.E. Te-Gómez. ECOSUR P2828 (1) Laguna de Alvarado, St. 8 (18°45'20.34"N, 95°46'29.04"W), December 6 2012, in rocks, Coll. J.M. Aguilar-Camacho. ECOSUR-OH-P0760 (23), Las Barrillas, St. 4 (18°11'20.15"N, 94°35'56.97"W), December 5 2012, on *C. virginica* culture, Coll. J. Cruz-Terrón. ECOSUR-OH-P0761 (15), Laguna Grande, Mandinga, St. 28 (19°1'54.96"N, 96°4'8.10"W), December 10 2012, on oyster, 11.41‰, 27.24 °C, Coll. T.F. Villalobos-Guerrero, MA. Tovar-Hernández, J.M. Aguilar-Camacho. ECOSUR-OH-P0762 (3), Laguna Grande, Mandinga, St. 26 (19°2'20.64" N 96°4'24.24"W), December 10 2012, on mangrove and oyster, 10.74 ‰, 26.63 °C, Coll. J.M. Aguilar-Camacho, T.F. Villalobos-Guerrero. UANL-3918 (6), Estero Casitas, Nautla, March 25 1990, Coll. A. Contreras-Arquieta.

Neotype locality. Mouth of Actopan River (19°25'2.95"N, 96°19'32.28"W), Gulf of Mexico, in *C. virginica* (Gmelin) reef, in muddy sediment, 1 m depth.

Description. Neotype complete (ECOSUR 0172), atokous female. Body tapering, 38 mm long, 2.1 mm wide, 74 chaetigers, filled with oocytes. Body yellowish, reddish brown pigmentation present dorsally on first quarter of body, discoloring towards midbody chaetigers; lateral oblique pale lines along chaetigers 1–9 (Fig. 1A), replaced by fingerprint-like lines from chaetiger 10 (Fig. 6L), anterior margin of segments with thin transverse band (Fig. 1A). Prostomium with pigmentation reddish brown along inner half of palps and around eyes; two broad hourglass-shaped lines extending from antennae towards eyes, separated by a thin pale line and two oval patches, one on each side of darker areas (Fig. 1A). Peristomium pigmented, pale lines present (Fig. 1A).

Prostomium 1.5 times longer than wide; antennae cirriform, slightly passing palps; eyes subequal, black, in trapezoidal arrangement (Fig. 1A). Peristomium three times longer than first chaetiger; tentacular cirri with short ceratophores; dorsal cirri longer than ventral ones, longest posterodorsal cirri reaching chaetiger 6 (Fig. 1A).

Pharynx dissected; jaws light brown with 11 rounded teeth, extending to base (Fig. 1G). Maxillary ring: I = 12 cones in triangle, II = 32–31 cones in arc, III = 50 cones in an ellipse, IV = 34–32 cones in arc. Oral ring: V = 1 cone, VI = 4–4 pyramids in diamond, VII–VIII = 42 in two irregular rows, P-bars alternating with small pyramids in anterior-most row, similar-sized pyramids alternating in posterior-most row (in everted pharynx).

Parapodial cirri pattern: Dorsal cirri longer than upper dorsal ligules throughout body; basally inserted on anterior region, displaced medially on midbody and posterior chaetigers. Ventral cirri shorter than neuropodial ligules throughout body, longer in few anterior chaetigers, basally inserted on anterior region, progressively distant throughout body.

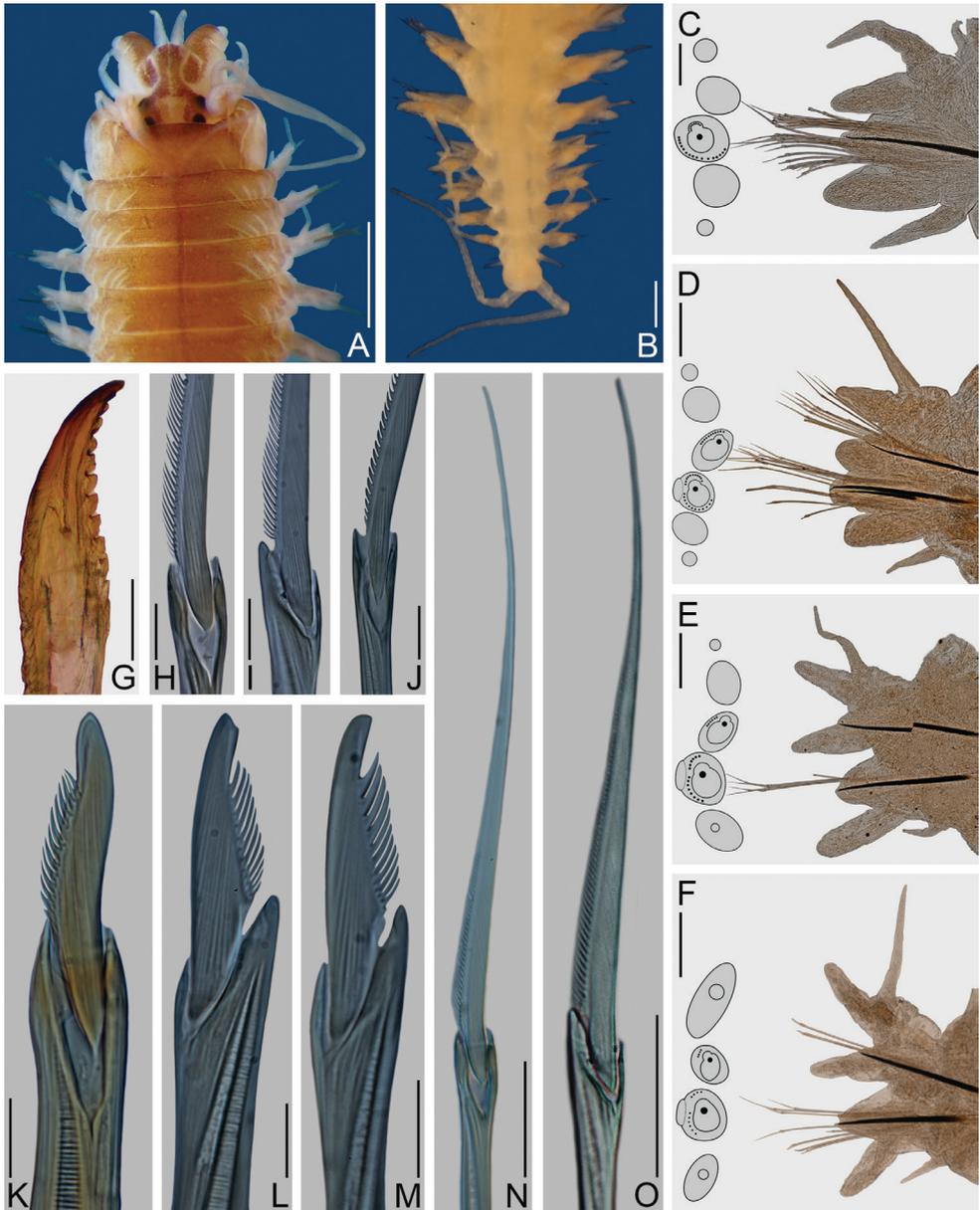


Figure 1. *Nereis oligohalina*. Neotype female **A–G** (ECOSUR 0172); paraneotypes **H–O** (ECOSUR 0173). **A** Anterior end, dorsal view **B** Posterior end, dorsal view **C** Parapodium 2, anterior view **D** Parapodium 10, anterior view **E** Parapodium 46, anterior view **F** Parapodium 64, anterior view **G** Left jaw, dorsal view **H** Supra-acicular homogomph spiniger, parapodium 40 **I** Sub-acicular heterogomph spiniger, from same **J** Supra-acicular homogomph spiniger, from same **K** Notopodial homogomph falciger, from same **L** Supra-acicular heterogomph falciger, parapodium 28 **M** Sub-acicular heterogomph falciger, from same **N** Notopodial homogomph spiniger, parapodium 40 **O** Sub-acicular heterogomph spiniger, from same. Scale bars: 1 mm (**A**); 0.3 mm (**B, G**); 50 μ m (**C**); 0.1 mm (**D–F**); 10 μ m (**H–M**); 30 μ m (**N, O**).

First two chaetigers uniramous, remaining ones biramous. Uniramous parapodia (Fig. 1C) with dorsal cirri basal, slightly longer than dorsal ligules. Dorsal ligules digitate; neuroacicular ligules subconical, subequal to dorsal ones; neuropodial ventral ligules digitate, slightly longer and basally twice as broad as dorsal ones. Ventral cirri slightly shorter than neuropodial ventral ligules; both dorsal and ventral cirri with similar width.

In anterior parapodia (Fig. 1D), dorsal cirri medial, slightly longer than notopodial dorsal ligules, extending beyond their tips. Notopodial dorsal ligules subconical; subequal to ventral ones; notopodial ventral ligules globose, notoacicular papillae conspicuous. Neuroacicular ligules globose, postchaetal lobes rounded, slightly shorter than neuroacicular ligules; neuropodial ventral ligules digitate, slightly shorter than neuroacicular ones. Ventral cirri shorter than neuropodial ligules; both dorsal and ventral cirri with similar width.

In middle and posterior parapodia (Fig. 1E, F), dorsal cirri medial, slightly shorter than notopodial dorsal ligules. Notopodial dorsal and ventral ligules subequal, subconical, longer than wide, notoacicular papillae conspicuous in middle parapodia only. Neuroacicular ligules subconical, wider than long, postchaetal lobes rounded, about half as long as neuroacicular ligules; neuropodial ventral ligules digitate, 3–4 times longer than wide, medially attached to neuroacicular ligules, 2–3 times longer than them. Ventral cirri half as long or one-third as long as neuropodial ventral ligules; dorsal and ventral cirri with similar width. Glandular masses slightly conspicuous on ligules in posterior parapodia (Figs 1F, 6Q).

In anterior and midbody parapodia notochaetae homogomph spinigers; neurochaetae homogomph spinigers and heterogomph falcigers in supra-acicular fascicles, heterogomph spinigers and falcigers in sub-acicular fascicles. In posterior parapodia, notochaetae homogomph spinigers and falcigers; neurochaetae as in anterior parapodia. Chaetae decreasing rapidly in number toward posterior end.

Notopodial homogomph spinigers pectinate (i.e. blade narrow with parallel teeth), teeth decreasing distally (Fig. 1N). Notopodial homogomph falcigers with sigmoidal blade, pectinate, distal tooth recurved, fused to blade (Fig. 1K). Neuropodial homogomph spinigers pectinate (Fig. 1H) or basally serrated (i.e. blade small with coarse teeth) (Fig. 1J), heterogomph spinigers pectinate (Fig. 1I); spinigers of similar size, teeth decreasing in size distally (Fig. 1N, O). Neuropodial heterogomph falcigers pectinate, distal tooth recurved, fused to blade, supra-acicular falcigers slightly broader than sub-acicular ones (Fig. 1L, M).

Pygidium not modified; anal cirri cirriform, as long as last 5–6 chaetigers (Fig. 1B).

Epitokes. Male fully transformed (ECOSUR-OH-P0761) complete; body tapering, 9 mm long, 0.9 mm wide, 57 chaetigers. Partially transformed male (ECOSUR P2827) complete; body tapering, 38 mm long, 2.1 mm wide, 57 chaetigers. Partially transformed female (ECOSUR P2827) complete; body tapering, 20 mm long, 1.6 mm width, 55 chaetigers. All with body yellowish with brown pigmentation present dorsally on first quarter of body, discoloring towards midbody chaetigers; faint lateral lines (Fig. 2A, D, E). Prostomium with pigmentation as in atokes, but less intense (Fig. 2B).

Prostomium longer than wide; antennae cirriform, slightly wider than those present in atokous female, as long as palps; eyes subequal, two (Fig. 2D) or three times (Fig. 2B) larger than antennal basal width, black, in trapezoidal arrangement (Fig. 2B, D).

Peristomium twice as long as first chaetiger, slightly pigmented; tentacular cirri present; dorsal tentacular cirri longer than ventral ones, posterodorsal ones reaching to chaetiger 10 (Fig. 2B, D).

Fully transformed male with pharynx everted, jaws amber with 10 teeth, inner edge toothed throughout. Maxillary ring: I = 8 cones in triangle, II = 30–32 cones in arc, III: 40 cones in rectangle, IV: 28–28 pointed cones in arc. Oral ring: V = 1 cone, VI: 4–4 pyramids in diamond, VII–VIII: 46 in two irregular rows, pyramids alternating with small cones in most-anterior row, pyramids with similar size alternating in most-posterior row.

Male body divided into two regions (Fig. 2A). Pre-natatory region includes chaetigers 1–16, natatory region from chaetiger 17 to end of body. Partially transformed female divided into two inconspicuous regions, parapodial lamellae visible from chaetiger 24.

Parapodial cirri pattern: Anterior parapodia with dorsal cirri modified in chaetigers 1–7 in males, 1–5 in females; ventral cirri modified in chaetigers 1–5 in males, 1–4 in females; modification attenuated in females. Dorsal cirri subequal to upper dorsal ligules in anterior chaetigers, slightly longer throughout body; basally inserted in anterior-most region, displaced medially toward end of body. Ventral cirri shorter than neuropodial ventral ligules in unmodified chaetigers, subequal in modified region; basally inserted in anterior region, barely displacing ventrally throughout body.

Chaetigers 1–2 uniramous (Fig. 2F); modified dorsal cirri basal, subpyriform (i.e. basally broad, medially broader, distally narrow), slightly longer than dorsal ligules. Dorsal and neuropodial ventral ligule subequal, subconical. Neuroacicular ligule subconical, much shorter than ventral one; postchaetal lobes rounded. Modified ventral cirri subpyriform, subequal to neuropodial ventral ligule; both dorsal and ventral cirri with similar width.

Chaetigers 3–7 in males (Fig. 2G) and 3–5 in females, with slightly modified biramous parapodia. Modified dorsal cirri medial, cattail-like (i.e. basal section broad, long; cirrostyle markedly narrower), slightly longer than notopodial dorsal ligules, extending beyond them; basal section 2–3 longer than distal one. Notopodial dorsal ligules subconical, subequal to notopodial ventral one; notopodial ventral ligule subconical, notoacicular papilla conspicuous. Neuroacicular ligule subconical, postchaetal lobe rounded, shorter than neuroacicular ligule; neuropodial ventral ligule digitate, as long as neuroacicular one (Fig. 2G). Modified ventral cirri cattail-like, subulate in chaetigers 6–7 in males and 5 in females, shorter than neuropodial ventral ligules; modified dorsal and ventral cirrus with similar width.

Chaetigers 8–16 in males and 6–23 in females with parapodial proportions as in atokes, but with more acute ligules (Fig. 2H).

Remaining parapodia biramous, modified (Fig. 2I, J, L, M). Dorsal cirri medial, subulate, ventral margins sinuate in males only, longer than notopodial ligules; ba-

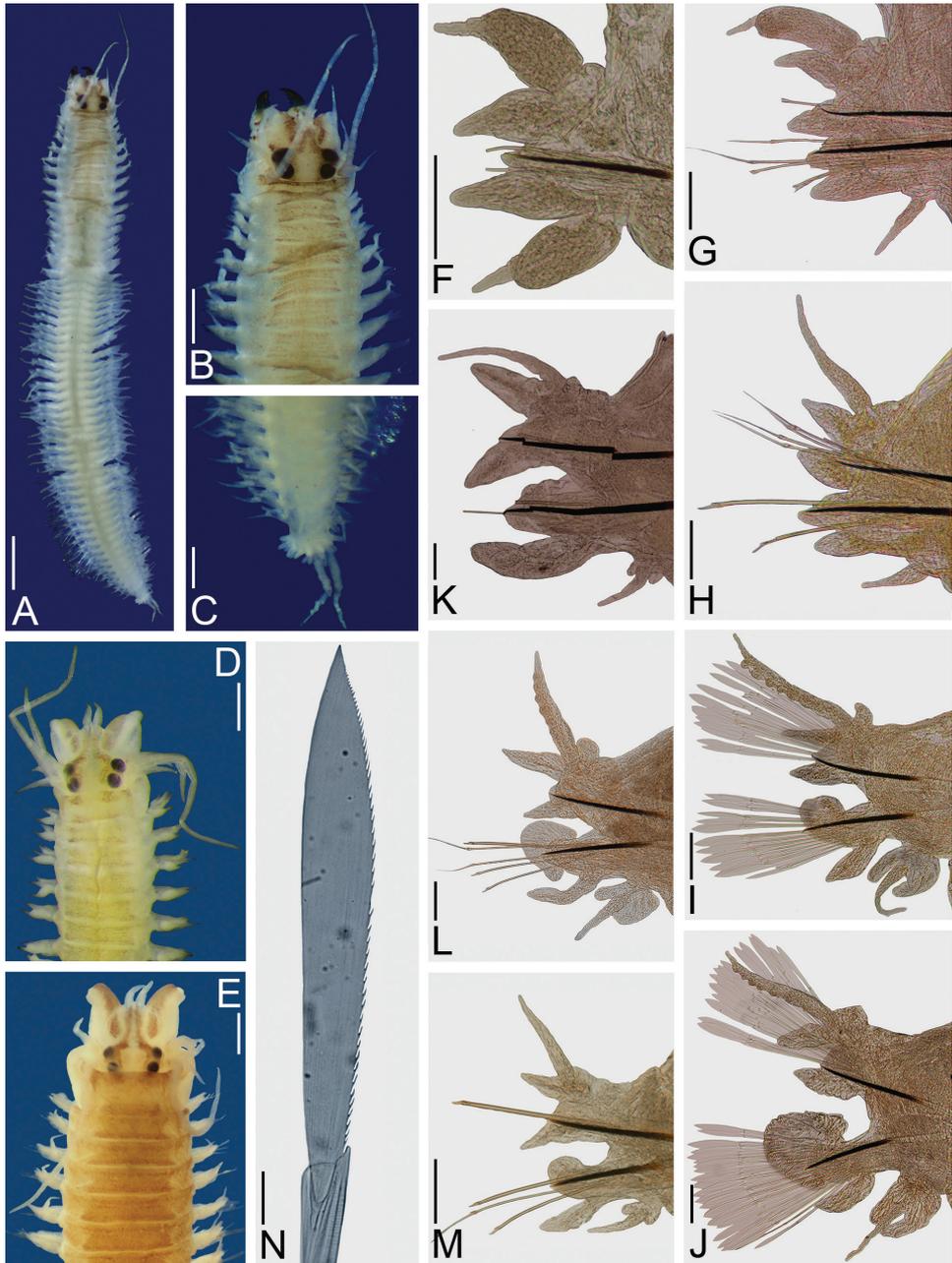


Figure 2. *Nereis oligobalina*. Non-type male **A–C, F–J, N** (ECOSUR–OH–P0761); non-type partially transformed male **D, L–M** (ECOSUR P2827); non-type partially transformed female **E, K** (ECOSUR P2827). **A** Whole specimen, dorsal view **B** Anterior end, dorsal view **C** Posterior end, dorsal view **D, E** Anterior ends, dorsal view **F** Parapodium 1, anterior view **G** Parapodium 6, anterior view **H** Parapodium 10, frontal view **I** Parapodium 18, anterior view **J** Parapodium 31, anterior view **K** Parapodium 10, anterior view **L** Parapodium 24, anterior view **M** Parapodium 52, anterior view **N** Sesquigomph natatory chaetae, parapodium 31. Scale bars: 1 mm (**A, D–E**); 0.5 mm (**B**); 0.2 mm (**C**); 0.1 mm (**F–M**); 10 μ m (**N**).

sal lamellae small, smallest in females, progressively smaller toward posterior region. Notopodial dorsal and ventral ligules subequal, subconical, notoacicular papillae conspicuous; ventral ligules with lamellae without projections along ventral margins. Neuroacicular ligules subconical, subequal to notopodial ventral ones; postchaetal lobes developing into flabellate lamellae, increasing in size posteriorly, decreasing in posterior-most chaetigers, some with slight projections in dorsal or ventral edge; neuropodial ventral ligules digitate, medially attached to neuroacicular ones. Ventral cirri subulate, subequal to neuroacicular ligules, with two basal lamellae of different sizes; dorsal cirri wider than ventral ones.

Prenatatory region with noto- and neurochaeta as in atokes, homogomph falcigers not observed, blades missing in most chaetae, number progressively reduced. In natatory region, noto- and neurochaetae sesquigomph chaetae with finely serrated, paddle-like blades (Fig. 2N).

In fully transformed males pygidium with anus surrounded by rosette of papillae (Fig. 2C); anal cirri sinuous, as long as last 5–6 chaetigers (Fig. 2C).

Transformation in females discrete; small lamellae on base of dorsal cirri, neuroacicular ligules and ventral cirri (Fig. 2K); size of lamellae increasing toward posterior end and becoming inconspicuous in far posterior chaetigers; other features as in atokous female.

Variation. The results of the analysis of body variation and paragnath numbers are summarized in Tables 1 and 2. The effect of fixation techniques on the shape of specimens have been recently evaluated by Oliveira et al. (2010) for *Laeonereis acuta* (Treadwell, 1923). The authors concluded that techniques of fixation can influence the shape and body proportions, especially if specimens were not previously relaxed, leading to erroneous identifications.

In the case of *N. oligohalina*, fixation with 96% ethanol clearly affected the anterior portion of specimens with strong contraction of first segments, hence the tentacular cirri can reach more posterior chaetigers but without modifying their lengths, reaching up to chaetiger 14 (Table 1). Differences are not significant for L_{10} , W_3 and W_{10} ($P = >0.05$), but significant for L_3 and rTC ($P = <0.001$, $P = <0.0001$). Maximum rTC for formalin specimens was preferred for the identification key because the data were less variable (Table 1). Nevertheless, these differences would not cause misidentification, because parapodial topology is not affected appreciably. Also pigmentation is very useful for recognizing the species.

In the maxillary ring, area I showed the least variation (Fig. 6J), and in oral ring areas V and VI rarely vary in one paragnath only (Fig. 6K), such that these areas can be regarded as the most stable ones. The fingerprint-like pattern starts in chaetigers 10–11 (Fig. 6L); it is size-independent, but in smaller specimens this pattern is faint; however, as shown below it is absent in the two other species. The divergence between parapodial rami reported by Rioja (1946) is evident in posterior chaetigers but only in some specimens, forming a furrow (Fig. 6O). Glandular masses appear more visible and also on neuropodial ligules (Fig. 6Q); perhaps these glands fade in specimens fixed with formalin, such as the type material. In mature specimens, the natatory region starts in chaetiger 15–17 in males, and 24–25 in females.

Table 1. Ranges, means and standard deviation of some body measures in three *Nereis* species (TL: total length, L_3 and L_{10} : length at chaetiger 3 and 10, respectively; W_3 and W_{10} : width at chaetiger 3 and 10, respectively; nC: number of chaetigers; rTC: reach of largest tentacular cirrus; SD: standard deviation).

<i>Nereis oligohalina</i>		TL	L_3	L_{10}	W_3	W_{10}	nC	rTC
Formalin specimens (n = 23)	Minimum	10.0	1.1	1.6	0.6	0.6	55.0	4
	Maximum	40.0	3.0	6.3	2.2	1.9	80.0	7
	Mean	24.8	2.3	3.8	1.6	1.4	66.9	5.7
	SD	9.3	0.5	1.3	0.5	0.4	7.8	0.9
Ethanol specimens (n = 19)	Minimum	9.0	0.6	1.5	0.7	0.6	57.0	5
	Maximum	36.0	3.0	6.5	2.2	2.0	78.0	14
	Mean	20.4	1.5	3.5	1.4	1.3	67.0	9.3
	SD	9.3	0.6	1.3	0.5	0.5	8.8	2.5
<i>N. garwoodi</i>		TL	L_3	L_{10}	W_3	W_{10}	nC	rTC
Formalin specimens (n=33)	Minimum	9.0	0.7	2.4	1.0	0.8	46.0	6
	Maximum	36.0	3.0	6.9	2.0	2.1	96.0	13
	Mean	22.1	1.8	3.8	1.5	1.5	72.7	9.3
	SD	9.4	0.5	1.0	0.3	0.3	11.8	1.5
<i>N. confusa</i> sp. n.		TL	L_3	L_{10}	W_3	W_{10}	nC	rTC
Formalin specimens (n=20)	Minimum	13.0	1.4	2.6	1.0	0.9	66.0	4
	Maximum	35.0	2.5	5.8	1.9	1.7	89	7
	Mean	24.5	1.8	4.0	1.5	1.3	78.6	5.3
	SD	6.6	0.4	0.9	0.3	0.3	6.0	0.9

Remarks. *Nereis oligohalina* (Rioja, 1946) is considered as a widespread species and even amphiameric, but this stems from taxonomic confusion and the lack of type material. Designation of a neotype for *N. oligohalina* was considered necessary because there are no type specimens and being a problematic species, there must be an objective definition for it (ICZN 1999, Art. 75.1). Consequently, a neotype has been selected, described and illustrated (ICZN 1999, Art. 75.3.3); this neotype fits the original description by Rioja (1946) (ICZN 1999 Art. 75.3.5). Because Rioja did not designate holotype, his material became syntypes and the species had two type localities (ICZN 1999 Art. 73.2.3, 76.1): Estero de Larios, Tecolutla, and El Cocal, Estero Casitas, both in Veracruz, Mexico. Although topotypic specimens from Estero Casitas are available, they are in poor condition, and therefore better specimens collected from nearby Actopan River were preferred once they were shown to conform to the same species (ICZN 1999, Recomm. 75A). The proposed neotype was collected in a similar environment and on oysters, as the original specimens (ICZN 1999, Art. 75.3.6); but the neotype locality is modified accordingly (ICZN 1999, Art. 76.3). The neotype was deposited in ECOSUR (ICZN 1999, Art. 75.3.7), including ‘paraneotypes’ and part of the additional material.

Neanthes oligohalina Rioja, 1946 was correctly transferred to *Nereis* by Hartman (1951) because there are notopodial homogomph falcigers in posterior chaetigers. Hart-

man (1951, 1954) suggested that *N. oligohalina* was 'inseparable' from *N. pelagica occidentalis* Hartman, 1945, but not synonymized. Salazar-Vallejo (1989) noted that although Rioja clearly recognized the presence of notopodial homogomph falcigers, he maintained the species under *Neanthes*, even in later publications (Rioja 1947, 1960, 1962).

The first synonymy involving these species was made by Pettibone (1956); she considered *N. p. occidentalis* different from *N. pelagica* and raised it to species level as *Nereis (Nereis) occidentalis* Hartman. Also, she regarded *Neanthes oligohalina* as a junior synonym of *N. occidentalis* being regarded as a variety. The detailed description provided by Pettibone allowed us to recognize differences in comparison to the Laguna Madre, Texas specimens. She recognized slight but important differences among these variants, mainly in paragnath number in areas V and VI; adding the relative size of neuropodial ligules in middle and posterior chaetigers. In the same work, she determined that *Nereis largoensis* Treadwell, 1931 was a junior synonym of *N. pelagica*, and that other material identified as *N. largoensis* based upon material examined by Treadwell corresponds to *N. occidentalis* (Pettibone 1956). We follow, however, González-Escalante and Salazar-Vallejo (2003), who concluded that these three species are not synonyms.

Nereis oligohalina differs from *N. occidentalis* in some diagnostic features. In *N. oligohalina* there are 8–15 paragnaths on area I and 1–2 on area V, whereas in *N. occidentalis* there are 2–3 paragnaths on area I and no paragnaths on area V. Further, in *N. oligohalina* neuropodial ventral ligules are 2–3 times longer than neuroacicular ligules, but in *N. occidentalis* neuropodial ventral ligules from posterior chaetigers are shorter than neuroacicular ones. Regarding chaetae, and as an additional difference, in *N. oligohalina* the notopodial homogomph falciger has the distal tooth less developed than in *N. occidentalis*.

Another synonymy was made by Day (1973), who regarded *N. pelagica occidentalis* Hartman and *N. occidentalis fide* McCloskey as junior synonyms of *Nereis falsa* de Quatrefages, 1865; however, in the list of synonyms of these two species he did not include Pettibone (1956), therefore *N. oligohalina* was not considered by him. *Nereis falsa*, has a rather complex or confusing delineation; according to Fauvel (1923) it differs from similar species by having different numbers of paragnaths in areas I and V, and different proportions in parapodial ligules. In fact, *N. falsa* is another species regarded as widely distributed and requires a critical revision and we could anticipate a restriction of its distribution to the Mediterranean region because its type locality is the Black Sea.

On the other hand, *N. oligohalina* has been recorded along American Atlantic coasts from northeastern Brazil, chiefly in ecological (community assemblages on *Spartina alterniflora* and mangroves), or population studies (secondary production and population dynamics), as well as part of taxonomic or genetic studies (Amaral et al. 2012). A detailed record was made by Santos and Lana (2003); unfortunately, a commentary and one plate was based upon specimens collected in Todos Los Santos Bay, and indicated that their material agrees with the original description regarding neuropodial ventral ligules in posterior parapodia, and the feature was less developed in specimens from other localities but were regarded as the same because the prostomial

pigmentation and paragnath number remained constant (Santos and Lana 2003). Lana et al. (2006) however, considered their previous record as a probable misidentification requiring a revision. Liñero-Arana and Díaz (2007) recorded *N. oligohalina* from Venezuela in La Restinga Lagoon, Margarita Island, associated with *Crassostrea rhizophorae* (Guilding), and recognized that their specimens resembled Brazilian ones and differed from those described by Rioja, mainly in parapodial morphology. These two publications pointed out the need for a revisionary work, recognizing *N. oligohalina* as valid species, but that their specimens were probably not the same as those described from Mexico because of parapodial features; at least the specimens from South America were regarded as a different species that should be clarified elsewhere.

Records of *N. oligohalina* from the Eastern Tropical Pacific (Berkeley and Berkeley 1958, 1960) belong to a new species described below.

Habitat. The species is associated with red mangrove *Rhizophora mangle* and with oysters. It has been found in Gulf of Mexico estuaries, including Tecolutla, Casitas-Nautla and Actopan (these estuaries have sand bars in their respective mouth rivers), and from coastal lagoons such as Mandinga and La Mancha. These systems have direct connection with the sea, some with seasonal closure of their mouths, with polyhaline to mesohaline waters (Lara-Domínguez et al. 2011).

The neotype and associated specimens were found in *Crassostrea virginica* (Gmelin) reef, in the Actopan river mouth. The specimens studied by Rioja (1946) from the Tecolutla estuary were found on mangrove roots covered by cirripedians, whereas specimens from the Casitas-Nautla estuary were collected between oysters (possibly *C. virginica*) and mytilids as *Ischadium recurvum* (Rafinesque) (reported as *Mytilus recurvatus* (sic) by Rioja); as Rioja indicated, *N. oligohalina* specimens cohabit with an *Alitta* species in the Actopan river mouth. This species has been reported as *N. occidentalis* Hartman, together with *Polydora websteri* Hartman, as epifauna of *C. virginica* (Ruiz-Guerrero and López-Portillo Guzmán 2006), and on *Rhizophora mangle* roots (Ruiz and López-Portillo 2014), from La Mancha.

Distribution. Restricted to the southwestern Gulf of Mexico.

***Nereis garwoodi* González-Escalante & Salazar-Vallejo, 2003**

Figures 3, 4, 6B, E, M, I, R

Nereis garwoodi González-Escalante and Salazar-Vallejo 2003: 156–160, figs 1a–k, 2a–h.

Type material. Quintana Roo, Mexico. Lectotype ECOSUR 0065 and paralectotypes ECOSUR 0066 (7), Chetumal (18°29'38.88"N, 88°17'22.89"W), Chetumal Bay, 1 m depth, in calcareous sedimentary rocks, mixed bottom, September 24 1999, Coll. L.E. González-Escalante, S.I. Salazar-Vallejo.

Additional material. Chetumal Bay, Quintana Roo, Mexico. ECOSUR P2829 (3), Alacranes (18°34'28.51"N, 88°14'24.21"W), May 1 1999, Coll. LEGE, SISV.

ECOSUR P2830 (14), Chetumal, May 3 1999, Coll. LEGE, SISV. ECOSUR P2831 (29), Chetumal, 21 May 1999, Coll. LEGE, SISV. ECOSUR P2832 (17), Alacranes (18°34'28.51"N, 88°14'24.21"W), May 21 1999, Coll. LEGE, SISV. ECOSUR P2833 (2), Luis Echeverría (18°39'04"N 88°12'07"W), May 21 1999, Coll. LEGE, SISV. ECOSUR P2834 (28), Chetumal (18°29'38.88"N, 88°17'22.89"W), June 30 1999, Coll. LEGE, SISV. ECOSUR P2835 (9), Chetumal (18°29'38.88"N, 88°17'22.89"W), August 27 1999, Coll. LEGE, SISV.

Type locality. Chetumal Bay, Mexico, Caribbean Sea, on rocks in mixed bottoms, 1 m depth.

Description. Lectotype complete (ECOSUR 0065), atokous female, damaged with incisions at level of chaetigers 1, 15, and 30. Body tapering, 36 mm long, 1.7 mm wide, 95 chaetigers. Body pale, pigmentation faint, brown rectangle present dorsally on middle of anterior chaetigers, striated, discoloring toward end of body, lateral pale lines in anterior chaetigers only, oocytes present. Prostomium with brown pigment along inner margins of palps, two lines extending from antennae toward anterior pair of eyes separated by a longitudinal pale area, and two oval lateral patches; peristomium slightly pigmented, pale lines present (Fig. 3A).

Prostomium 1.5 times longer than wide; antenna cirriform, slightly passing palps; eyes subequal, black, in a rectangle (Fig. 3A). Peristomium twice longer than first chaetiger; tentacular cirri with short ceratophores, left cirri broken; dorsal longer than ventral ones, posterodorsal ones reaching chaetiger 12 (Fig. 3A).

Pharynx everted, jaws pale brown with 13 rounded teeth, extending to base (Fig. 3I). Maxillary ring: I = 15 pyramids in diamond, II = 31–31 pyramids and cones in arc, III = 44 cones in an ellipse, IV = 35–35 pyramids in arc (Fig. 3A). Oral ring: V = 1 cone, VI = 4–4 pyramids in diamond, VII–VIII = 42 in two irregular rows, P-bars alternating with small pyramids in anterior-most row, pyramids and cones with similar size alternating in posterior-most row.

Parapodial cirri pattern: Dorsal cirri longer than upper dorsal ligules throughout body; basally inserted on anterior region, displaced medially in midbody region, becomes subdistal in posterior chaetigers. Ventral cirri longer than neuropodial ligules in a few anterior chaetigers, progressively reduced throughout body; basally inserted on anterior region, barely migrating ventrally throughout body.

First two chaetigers uniramous, remaining ones biramous. In uniramous parapodia (Fig. 3D), dorsal cirri basal, slightly longer than notopodial ligules. Dorsal and neuropodial ventral ligules subequal, digitate, three times longer than neuroacicular ligules; neuroacicular ligules subconical, postchaetal lobes rounded. Ventral cirri subequal to neuropodial ventral ligules; both dorsal and ventral cirri with similar length and width.

In anterior parapodia (Fig. 3E), dorsal cirri medial, longer than notopodial ligules, extending beyond them. Notopodial dorsal ligules subconical, slightly longer than ventral ones; notopodial ventral ligules subconical, slightly longer than neuroacicular ligules, notoacicular papillae very conspicuous. Neuroacicular ligules subconical, subequal to ventral ones, postchaetal lobes rounded, slightly shorter than neuroacicular ligules; neuropodial ventral ligules digitate, basally attached to neuroacicular ligules.

Ventral cirri shorter than neuropodial ventral ligules; dorsal cirri twice wider than ventral ones.

In middle parapodia (Fig. 3F), dorsal cirri medial, as long as notopodial ligules, extending beyond them. Notopodial dorsal and ventral ligules subequal, subconical, notoacicular papillae inconspicuous. Neuroacicular ligules subconical, slightly shorter than remaining ones, postchaetal lobes rounded, shorter than neuroacicular ligules; neuropodial ventral ligules digitate, basally attached to neuroacicular ones. Ventral cirri half as long as neuropodial ligule; both dorsal and ventral cirri with similar width.

In posterior parapodia (Figs 3G, H), dorsal cirri medial, slightly longer than notopodial ligule. Notopodial dorsal ligules become broad, longer than ventral ones; notopodial ventral ligules become large, 2–3 times longer than neuroacicular ligules, notoacicular papilla inconspicuous. Neuroacicular ligules subconical, half as long as neuropodial ventral ones, postchaetal lobes inconspicuous; neuropodial ventral ligules digitate, basally attached to neuroacicular ligules. Ventral cirri up to half as long as neuropodial ligule; dorsal and ventral cirri with similar width. Glandular masses conspicuous on notopodial ligules.

In anterior and midbody parapodia, notochaetae homogomph spinigers; neurochaetae homogomph spinigers and heterogomph falcigers in supra-acicular fascicles, heterogomph spinigers and falcigers in sub-acicular fascicles. In posterior parapodia, notochaetae homogomph spinigers and falcigers; neurochaetae as in anterior parapodia. Number of chaetae decreasing toward posterior end.

Notopodial homogomph spinigers pectinate, teeth decreasing in size distally (Fig. 3O). Notopodial homogomph falcigers with sigmoid blade, pectinate, distal tooth incurved, fused to blade (Fig. 3C). Neuropodial homogomph spinigers pectinate or basally serrate (Fig. 3J), heterogomph spinigers pectinate (Fig. 3P); both with teeth decreasing in size distally. Neuropodial heterogomph falcigers pectinate, distal tooth incurved, fused to blade, supra-acicular slightly broader than sub-acicular (Fig. 3L–N); supra-acicular falcigers narrow in midbody chaetigers, becoming broad posteriorly (Fig. 3L, M).

Pygidium without modification; anal cirri cirriform, as long as last 4–5 segments (Fig. 3B).

Epitokes. Paralectotype fully transformed male (ECOSUR 0066) complete, body tapering, 9 mm long, 1 mm wide, 46 chaetigers; paralectotype partially transformed female (ECOSUR 0066) incomplete, body tapering, 16 mm long, 2 mm wide, 63 chaetigers; fully transformed female (ECOSUR P0066) complete, body tapering, 12 mm long, 1.6 mm wide, 63 chaetigers. All with body yellowish with brown pigmentation present dorsally on first quarter of body, discoloring toward midbody chaetigers (Fig. 4E, F). Prostomium and peristomium with pigmentation similar to atokes (Fig. 4A, B).

Prostomium longer than wide; antennae cirriform, as long as palps; eyes black, subequal, in a rectangle, three times larger than antennal basal width (Fig. 4A, B). Peristomium twice length of first chaetiger; tentacular cirri with short ceratophores, dorsal tentacular cirri longer than ventral ones, posterodorsal reaching to chaetiger 9 in male, 13 in female (Fig. 4A, B).

Male with pharynx everted, jaws amber with 9 teeth. Maxillary ring: I = 6 pointed cones in triangle, II = 19–20 pointed cones in arc, III = 28 pointed cones in rectangle, IV = 22–19 pointed cones in arc. Oral ring: V = 1 pointed cone, VI = 4–3 pyramids in diamond, VII–VIII = 42 in two irregular rows, P-bars alternating with small pyramids in most-anterior row, pyramids alternating with cones with similar size in most-posterior.

Male body divided into two regions (Fig. 4E); pre-natatory region includes chaetigers 1–16, natatory region from chaetiger 17 to end of body. Fully transformed female body with two regions; pre-natatory includes chaetigers 1–26, natatory region from chaetiger 27 to end of body (Fig. 4F). Partially transformed female divided in two inconspicuous regions, lamellae start in chaetiger 25.

Parapodial cirri pattern: Anterior parapodia with dorsal cirri modified in chaetigers 1–7 in males, 1–5 in females; ventral cirri modified in chaetigers 1–5 in males, 1–4 in females. Dorsal cirri subequal to upper dorsal ligules in anterior chaetigers, become subequal throughout body; basally inserted in most-anterior region, displaced medially throughout body. Ventral cirri shorter than neuropodial ligules in unmodified chaetigers, subequal in modified region; basally inserted in anterior region, barely migrating ventrally throughout body.

Chaetigers 1–2 with uniramous (Fig. 4G, L), modified dorsal cirri basal, subpyriform in males, cattail-like in females, subequal to dorsal ligules. Dorsal and neuropodial ventral ligules subequal, subconical, twice longer than wide in male, 1.5 times longer than wide in female. Neuropodial lobe subconical, shorter than dorsal ligules; postchaetal lobes rounded. Modified ventral cirri shorter than neuropodial ventral ligules; dorsal and ventral cirri subequal with similar width and length.

Chaetigers 3–7 in males (Fig. 4H) and 3–5 in females (Fig. 4M) with slightly modified biramous parapodia. Modified dorsal cirri medial, cattail-like, slightly longer than notopodial ligules, extending beyond them; broader section as long as narrower one. Notopodial dorsal ligules subconical, slightly longer than notopodial ventral ligules; notopodial ventral ligules subconical, twice longer than neuroacicular ligules, notoacicular papillae conspicuous. Neuroacicular ligules subconical, postchaetal lobes rounded; neuropodial ventral ligules digitate, longer than neuroacicular ones. Modified ventral cirri cattail-like, subulate in chaetigers 6–7 in males and 5 in females, shorter than neuropodial ventral ligules.

Parapodial proportions as in atokous from chaetigers 8–16 in male and 6–26 in female (Fig. 4I, N).

Remaining parapodia modified (Fig. 4J, K, O, P). Dorsal cirri medial, subulate, ventral margins sinuate in males only, subequal to notopodial ventral ligules; basal lamellae large in males, small in females, increasing size toward posterior chaetigers and decreasing in most-posterior ones.

Notopodial dorsal ligules subconical, longer than ventral ones in male, subequal in female; notopodial ventral ligules subconical, developing a large ventral lamella in males only, with a round projection. Neuroacicular ligules subconical, shorter than notopodial ventral ones; postchaetal lobes developing into flabellate lamellae with a round projection in dorsal edge in males, small lamellae in females, progressively in-

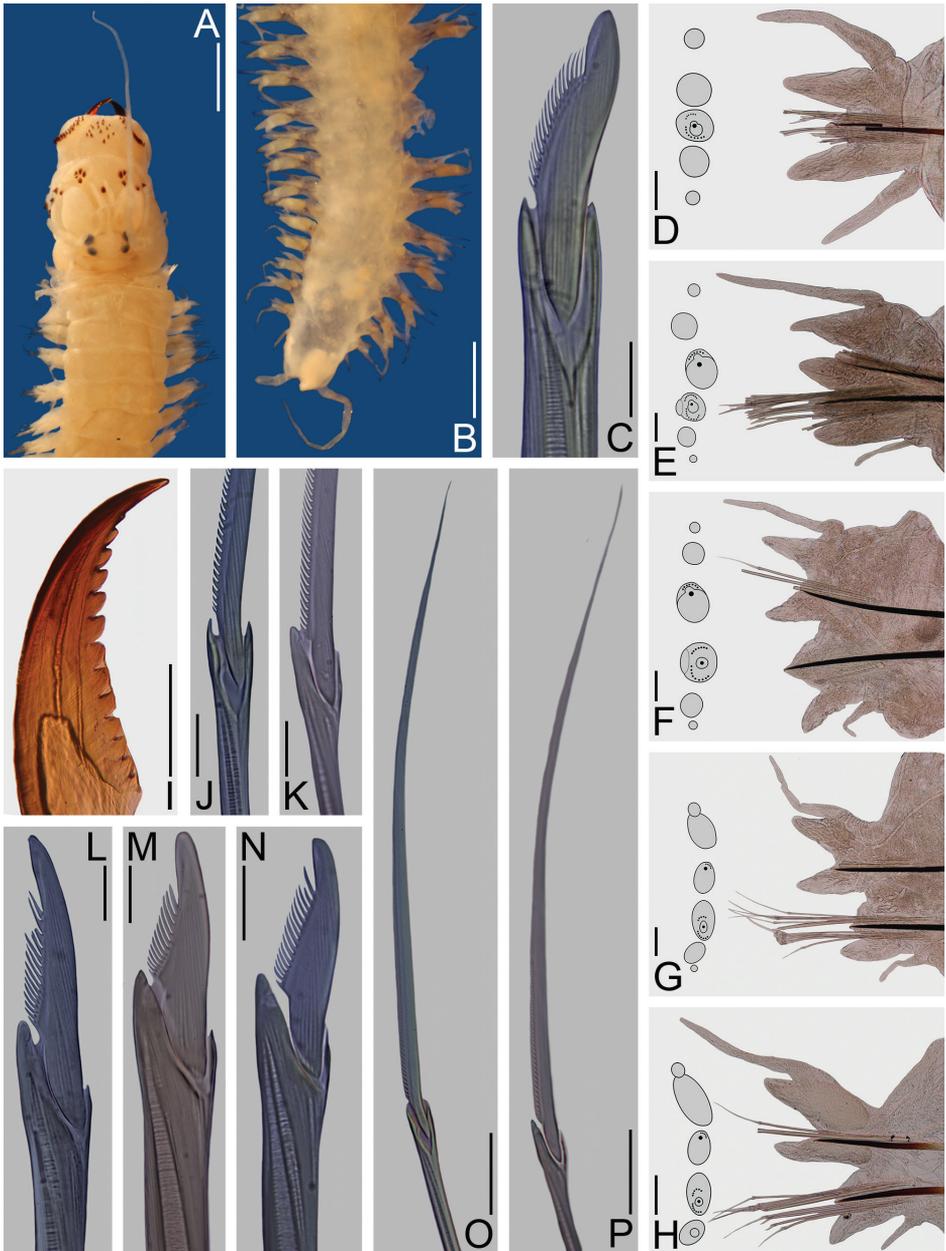


Figure 3. *Nereis garwoodi*. Lectotype female **A–B**, **D–P** (ECOSUR 0065); paralectotype **C** (ECOSUR 0066). **A** Anterior end, dorsal view **B** Posterior end, dorsal view **C** Notopodial homogomph falciger, parapodium 75 **D** Parapodium 2, anterior view **E** Parapodium 9, anterior view **F** Parapodium 28 **G** Parapodium 56, anterior view **H** Parapodium 80, anterior view **I** Left jaw, dorsal view **J** Supra-acicular homogomph spiniger, parapodium 80 **K** Sub-acicular heterogomph spiniger, from same **L** Supra-acicular heterogomph falciger, parapodium 56 **M** Supra-acicular heterogomph falciger, parapodium 80 **N** Sub-acicular heterogomph falciger, from same **O** Supra-acicular heterogomph spiniger, from same **P** Sub-acicular heterogomph spiniger, from same. Scale bars: 1 mm (**A–B**, **I**); 50 μm (**C**, **J–N**); 0.1 mm (**D–H**); 0.3 mm (**O–P**).

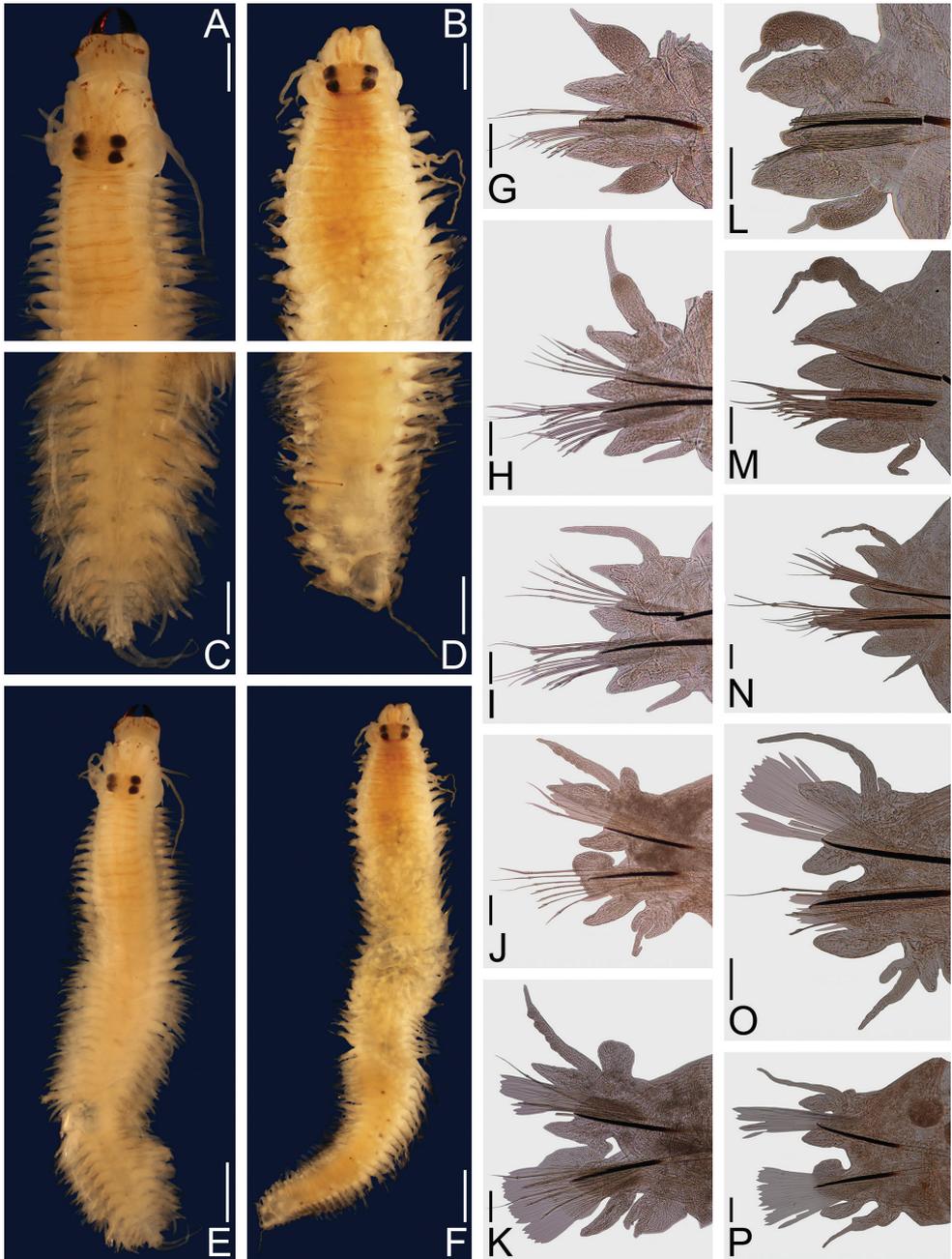


Figure 4. *Nereis garwoodi*. Paralectotype male **A, C, E, G–K** (ECOSUR 0066); paralectotype female **B, D, F, L–P** (ECOSUR 0066). **A, B** Anterior ends, dorsal view. **C, D** Posterior ends, dorsal view. **E, F** Whole specimens, dorsal view. **G** Parapodium 2, anterior view. **H** Parapodium 6, anterior view. **I** Parapodium 10, anterior view. **J** Parapodium 18, anterior view. **K** Parapodium 36, anterior view. **L** Parapodium 2, anterior view. **M** Parapodium 5, anterior view. **N** Parapodium 10, anterior view. **O** Parapodium 26, anterior view. **P** Parapodium 36, anterior view. Scale bars: **A–D** = 0.5 mm; **E–F** = 1 mm; **G–P** = 0.1 mm.

creasing in size and decreasing in far posterior segments; neuropodial ventral ligules digitate, basally attached to neuroacicular ones. Ventral cirri subulate, slightly longer than neuroacicular ligules, with two basal lamellae of different sizes; dorsal cirri wider than ventral ones.

Prenatatory region with noto- and neurochaetae as in atokes, homogomph falcigers not observed. In natatory region, notochaetae and neurochaetae sesquigomph chaetae with finely serrated, paddle-like blades; atokous chaetae not completely replaced in specimens of either sex, homogomph falcigers observed in male (Fig. 4J, K, O, P).

Pygidium modified, anus surrounded by rosette of papillae in male, unmodified in female (Fig. 4C, D); anal cirri cirriform, as long as last 5–6 segments (Fig. 4C, D).

Variation. The results of the analysis of body variation and analysis of paragnath numbers are summarized in Tables 1 and 2. The width measurements reported here differ from the original description because chaetiger width without parapodia was used, instead of measuring them including parapodia. The arrangement and number of paragnaths have similar ranges as those reported for *N. oligohalina* (Fig. 6B, E; Table 2); however, area I has a larger range, and the arrangement is somewhat variable, often in a triangle (Fig. 6I). Also, paragnaths are more robust than in *N. oligohalina* and *N. confusa* sp. n.

Regarding pigmentation, the striated rectangle seen in lectotype is more conspicuous in some specimens (Fig. 6M), which is also sometimes present in *N. oligohalina*, but the color is much more intense whereas the fingerprint-like pattern of the latter species was not observed. In mature specimens, the natatory region starts from chaetiger 17 only in males and 25–27 in females, which differs from the original description (22 in males and 21 in females). One specimen presented a duplicated ventral cirrus, but it was regarded as abnormal (Fig. 6R).

Remarks. González-Escalante and Salazar-Vallejo (2003) indicated that they had six atokes and two epitokes as syntypes. Five atokous syntypes were expected to be sent to four foreign museums, but were never dispatched. Further, these syntypes were not formally deposited and labeled, and parts of the descriptions and illustrations are too imprecise to enable separation of *N. garwoodi* from *N. oligohalina*.

In an attempt to redefine the species, a lectotype has been selected (ICZN 1999, Art. 74.1) to avoid future confusion; although the syntype series has better preserved specimens, the lectotype matches the original description and illustration, and was therefore preferred (ICZN 1999, Recomm. 74B). In order to ensure their validity, the term has been introduced in the material section and in the description (ICZN 1999, Art. 74.7.1, 74.7.3), and the lectotype has been described, illustrated and their data updated for its recognition (ICZN 1999, Art. 74.7.2, Recomm. 74C, 74E); the remaining syntypes are regarded as paralectotypes (ICZN 1999, Recomm. 74F). These specimens are deposited in ECOSUR.

Nereis garwoodi is closely allied with *N. oligohalina*, but they differ in some features in both atokous and epitokous forms, and in their habitats. In atokes, *N. garwoodi* never shows the dark brown coloration nor the fingerprint-like pattern found in *N. oligohalina*. The ranges of paragnath numbers of both species overlap and therefore are

Table 2. Ranges, means and standard deviations (SD) in number of paragnaths in three *Nereis* species (r: right, l: left).

	Pharynx areas									
	I	II-r	II-l	III	IV-r	IV-l	V	VI-r	VI-l	VII-VIII
<i>N. oligohalina</i> (n=27)										
Minimum	8	25	25	32	22	22	1	4	3	40
Maximum	15	38	37	71	45	39	2	4	4	47
Mean	11.7	31.0	30.4	49.1	31.5	31.4	1.04	4.0	3.9	43.9
SD	2.3	2.9	3.1	9.2	4.9	3.6	0.2	0.00	0.2	2.0
<i>N. garwoodi</i> (n=29)										
Minimum	4	19	20	28	22	19	1	4	3	42
Maximum	19	42	40	59	43	38	1	4	4	46
Mean	10.7	30.3	30.5	44.6	31.0	30.1	1.0	4.0	3.9	44.0
SD	3.4	5.3	5.7	6.4	5.3	4.5	0.00	0.00	0.3	1.3
<i>N. confusa</i> sp. n. (n=30)										
Minimum	4	30	28	39	34	35	1	3	3	42
Maximum	11	36	42	62	58	54	1	5	6	45
Mean	7.3	32.3	34.2	51.2	45.6	45.1	1	3.6	4.0	42.9
SD	2.1	2.3	3.9	8.1	8.9	6.6	0	0.7	0.9	1.1

not useful to separate them, and the relative length of tentacular cirri would be useful if fixation method is the same (Table 1).

In *N. garwoodi*, both dorsal and neuropodial ventral ligules are twice as long as neuroacicular ligules in uniramous chaetigers, whereas in *N. oligohalina* these are subequal and slightly longer, respectively. Also, in *N. garwoodi* the neuropodial postchaetal lobes are visible in the anterior and midbody only, whereas in *N. oligohalina* they are visible throughout body.

Further, *N. garwoodi* has notopodial ventral ligules twice as long as neuropodial ventral ones in posterior chaetigers, whereas in *N. oligohalina* these ligules are subequal to each other; further, in *N. oligohalina* neuropodial ventral ligules are medially attached in posterior chaetigers, whereas in *N. garwoodi* they are basally attached throughout body. Moreover, in *N. garwoodi* notopodial homogomph falcigers have more teeth and they are narrower than in *N. oligohalina*; also, in *N. garwoodi* the blades of supra-acicular heterogomph falcigers become broader and shorter in posterior chaetigers, but this modification is not present in *N. oligohalina*.

In epitokes, *N. garwoodi* has modified, cattail-like dorsal cirri present in biramous chaetigers with the basal sections as long as distal ones, whereas in *N. oligohalina* basal sections are longer. Also, in general *N. garwoodi* have better developed lamellae in natatory chaetigers than *N. oligohalina*, especially the basal lamellae of the dorsal cirri, the lamellae of both notopodial ventral and neuroacicular ligules. Moreover, epitokal transformation is more pronounced in females of *N. garwoodi* than in females of *N. oligohalina*. On the other hand, *N. garwoodi* is associated with calcareous rocks, while *N. oligohalina* is associated with reef-building bivalves and the mangrove *R. mangle*.

Habitat. Chetumal Bay is a semi-closed, dynamic system linked to the Caribbean Sea by several freshwater tributaries, having a salinity gradient ranging 7–18 practical salinity units (psu) (Carrillo et al. 2009). The species bores into calcareous sedimentary rocks, building mucous tubes, and has been regarded as a sedentary herbivore (González-Escalante and Salazar-Vallejo 2003); to obtain the specimens, rocks must be broken. Although the Bay has extensive zones of mangroves, *N. garwoodi* has never been found among them.

Distribution. Apparently restricted to Chetumal Bay. González-Escalante and Salazar-Vallejo (2003) report a gradient of decreasing abundance from the southern to the northern regions of the bay, probably related to organic matter load.

***Nereis confusa* sp. n.**

<http://zoobank.org/5048FF4A-0F6A-4B03-BCF5-352F41EDBC39>

Figures 5, 6C, F–H, N, P

Nereis (Neanthes) oligohalina Berkeley and Berkeley 1958: 402 (*non* Rioja, 1946).

Nereis oligohalina Berkeley and Berkeley 1960: 359 (*non* Rioja, 1946).

Type material. Gulf of California, Baja California Sur. Holotype ECOSUR 0174 and paratypes ECOSUR 0175 (5), Bahía de La Paz (24°08'38.68"N, 110°20'44.40"W), March 1 2004, 70 m from shore, on wrinkled pen shell *Pinna rugosa*, sponges, PVC tube, and filamentous green algae, Coll. M.A. Tovar-Hernández, P. Salazar-Silva.

Additional material. Gulf of California, Baja California. ECOSUR P2836 (16), Bahía de Los Ángeles (28°58'6.72"N, 113°32'43.24"W), Gulf of California, March 17 1985, on *Atrina maura*, Coll. E. Aguirre, C. Garza. **Gulf of California, Sinaloa.** ECOSUR P2837 (10), Estero el Yugo (23°18'8.30"N, 106°29'0.53"W), Mazatlán, February 24 2004, 50 cm depth, fine sediment, on filamentous green algae on mangrove roots, Coll. S. Rendón-Rodríguez, Nuri M., M.A. Tovar-Hernández, P. Salazar-Silva. **Baja California Sur.** ECOSUR P2838 (32), same data as holotype. ECOSUR P2839 (2), Bahía La Paz (24°12'6.51"N, 110°17'59.26"W), Gulf of California, March 2 2004, 1 m depth, on basalt rocks, sponges and algae, Coll. M.A. Tovar-Hernández, P. Salazar-Silva.

Etymology. The specific name (*L. confusa*: confused, perplexed, troubled) indicates an earlier problematic delineation of the species; it is a noun in apposition.

Description. Holotype complete (ECOSUR 0174), atokous female. Body tapering, 34 mm long, 1.7 mm wide, 81 chaetigers, immature. Body yellowish, reddish brown pigmentation present dorsally on first quarter of body as three spots pattern, two lateral ones, and the other less pigmented, middorsal, forming discontinuous transverse bands up to chaetiger 10, remaining segments pale; lateral pale lines in anterior chaetigers only (Fig. 5A). Prostomium with pigmentation brown on inner margins of palps and with two oval patches (Fig. 5A); peristomium dorsally pigmented, variegated (Fig. 5A), with very short pale lines on posterior margin.

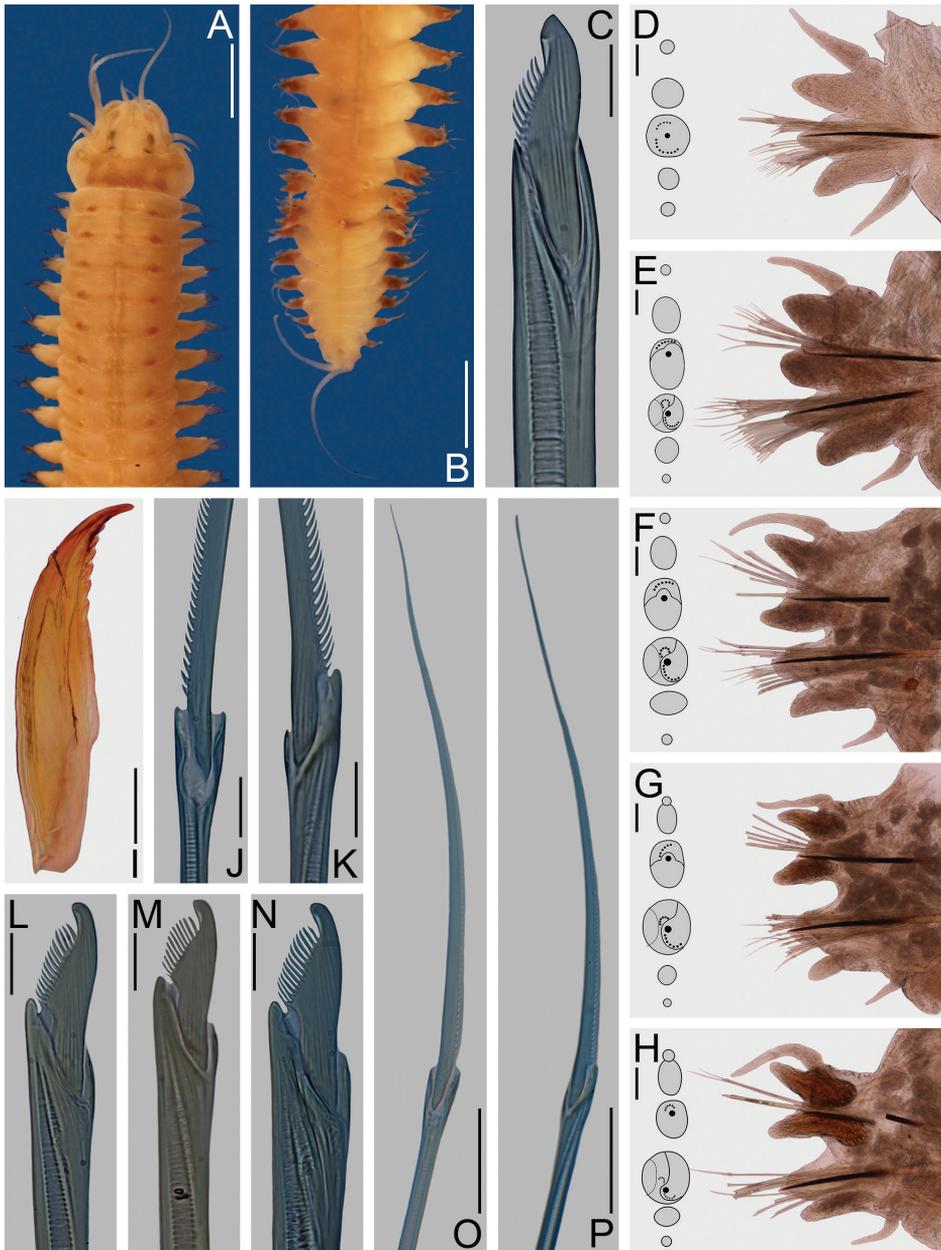


Figure 5. *Nereis confusa* sp. n. Holotype **A–P** (ECOSUR 0174). **A** Anterior end, dorsal view **B** Posterior end, dorsal view **C** Notopodial homogomph falciger, parapodium 72 **D** Parapodium 2, anterior view **E** Parapodium 11, anterior view **F** Parapodium 28, anterior view **G** Parapodium 51, anterior view **H** Parapodium 72, anterior view **I** Left jaw, dorsal view **J** Supra-acicular homogomph spiniger, parapodium 51 **K** Sub-acicular heterogomph spiniger from same **L** Sub-acicular heterogomph falciger from same **M** Supra-acicular heterogomph falciger, parapodium 72 **N** Supra-acicular heterogomph falciger from same **O** Supra-acicular homogomph spiniger from parapodium 51 **P** Sub-acicular heterogomph spiniger from same. Scale bars: 1 mm (**A–B**, **I**); 50 μ m (**C**, **J–N**); 0.1 mm (**D–H**); 0.3 mm (**O–P**).

Prostomium longer than wide; antennae cirriform, extending beyond palps; eyes subequal, black, in a rectangle (Fig. 5A). Peristomium twice longer than first chaetiger; tentacular cirri with short ceratophores, dorsal cirri longer than ventral ones, postero-dorsal ones reaching to chaetiger 5 (Fig. 5A).

Pharynx dissected, jaws with 8 teeth, restricted to anteromedial edge, light brown (Fig. 5I). Maxillary ring: I = 5 cones in rectangle, II = 30–30 cones in arc, III = 49 cones in an ellipse, IV = 41–36 cones and some merged, in sigmoidal. Oral ring: V = 1 cone, VI = 5–5 cones in round, VII–VIII: 42 in two irregular rows, P-bars and small cones alternating in most anterior row, pyramids and small cones in most-posterior row.

Parapodial cirri pattern: Dorsal cirri longer than upper dorsal ligules throughout body; basally inserted on anterior region, displaced medially on midbody and posterior regions. Ventral cirri as long as neuropodial ligules in a few anterior chaetigers, progressively reduced throughout body; basally inserted in anterior region, migrating ventrally throughout body.

First two chaetigers uniramous, remaining biramous. In uniramous parapodia (Fig. 5D), dorsal cirri basal, slightly longer than dorsal ligules. Dorsal ligules subconical; neuroacicular ligules subconical, subequal to dorsal ligules; neuropodial ventral ligules digitate, shorter than neuroacicular ligules. Ventral cirri subequal than neuropodial ligule; dorsal cirri slightly wider than ventral ones.

In anterior parapodia (Fig. 5E), dorsal cirri medial, as long as notopodial dorsal ligules, extending beyond them. Notopodial dorsal ligules subconical; notopodial ventral ligules globose, subequal to dorsal ones, notoacicular papillae conspicuous. Neuroacicular ligules subconical, postchaetal lobe rounded, subequal than neuroacicular ligules; neuropodial ventral ligules digitate, shorter than neuroacicular ones. Ventral cirri shorter than neuropodial ligule; dorsal cirri slightly wider than ventral ones.

In midbody and posterior parapodia (Figs 5F–H), dorsal cirri medial, subequal to notopodial dorsal ligules. Notopodial dorsal and ventral ligules subequal, slightly enlarged in posterior parapodia, subconical, longer than wide, notoacicular papillae conspicuous in middle parapodia. Neuroacicular ligules subconical, postchaetal lobes rounded, shorter than notopodial ligules; neuropodial ventral ligules digitate, slightly shorter than neuroacicular ones. Ventral cirri shorter than neuropodial ventral ligules; dorsal cirri slightly wider than ventral ones (Fig. 5F–H).

In anterior and midbody parapodia, notochaetae homogomph spinigers; neurochaetae homogomph spinigers and heterogomph falcigers in supra-acicular fascicles, heterogomph spinigers and falcigers in sub-acicular fascicles. In posterior parapodia, notochaetae homogomph spinigers and falcigers; neurochaetae as in anterior parapodia.

Notopodial homogomph spinigers pectinate, teeth decreasing in size distally. Notopodial homogomph falcigers pectinate, 9 teeth, distal tooth stout, incurved, fused to blade (Fig. 5C). Neuropodial homogomph spinigers basally serrate (Fig. 5J), heterogomph spinigers pectinate or serrate (Fig. 5K); both with teeth decreasing in size distally. Neuropodial heterogomph falcigers pectinate, distal tooth incurved, fused to blade, very conspicuous (Fig. 5L–N); in posterior parapodia with short (Fig. 5M) or long (Fig. 5N) blades in both fascicles, missing in most chaetae.

Pygidium with broad margin, anus crenulated; anal cirri cirriform, as long as last 3–4 segments (Fig. 5B).

Variation. The results of the analysis of body variation and paragnath numbers are summarized in Table 1 and 2. The arrangement and number of paragnaths is similar to that in *N. oligohalina* and *N. garwoodi*, but in *N. confusa* sp. n. paragnaths in areas III and IV are more numerous than in the other two species (Fig. 6C, F; Table 2), and cones have rounded tips; further, *N. confusa* sp. n. is the only species of the three with merged paragnaths.

All specimens examined show the same dorsal spotted pigmentation, but in some, especially the largest specimen, the middorsal spot disappears and only two discontinuous lines are visible along chaetigers 1–10; fingerprint-like or striated patterns were not observed. In mature specimens, the transformation starts in chaetiger 18 in males, 22 in females as previously noticed by Berkeley and Berkeley (1958, 1960).

Remarks. *Nereis confusa* sp. n. has been recorded as *N. oligohalina*; however, there are several differences between these two species. In *N. confusa* sp. n. the spotted pigmentation pattern extends up to chaetigers 10–14, and the jaws have 8 teeth restricted to the distal part of its inner edge, whereas in *N. oligohalina* the pale areas are replaced by fingerprint-like patterns from chaetiger 11, and its jaws have 11 teeth along its inner edge. Further, in *N. confusa* sp. n., both notopodial ligules and neuroacicular ligules are subequal to, or slightly longer than, neuropodial ventral ligules in midbody and posterior parapodia, whereas in *N. oligohalina*, they are twice as long as the neuroacicular ligules in midbody and posterior parapodia. On the other hand, *N. confusa* sp. n. has falcigers with broad blades, whereas in *N. oligohalina* they are narrower. Furthermore, in *N. confusa* sp. n. distal tooth of notopodial homogomph falciger is short and well developed, whereas in *N. oligohalina* it is longer and weakly developed.

The first records for *N. confusa* sp. n. (as *N. oligohalina*) from the Mexican Pacific were made by Berkeley and Berkeley; first, they reported *Nereis (Neanthes) oligohalina* males from Hipolito Bay (Berkeley and Berkeley 1958), and males and females from La Paz (Berkeley and Berkeley 1960). They argued that prostomium, anterior chaetigers and arrangement of paragnaths all matched Rioja's descriptions. In their brief comments, they indicated the start of the modified region or first epitokous parapodium (17 in males, 22 in females), and a spotted pattern of pigmentation in males. These features match with *N. confusa* sp. n. rather than *N. oligohalina*.

Rioja (1962) cited Berkeley and Berkeley (1958), and recorded *N. confusa* sp. n. (as *N. oligohalina*) from El Mogote, Ensenada de La Paz, Baja California Sur; he mentioned a slight discrepancy in number of paragnaths in area I, and that paragnaths in the periphery of area III were larger than the rest of the group forming a borderline; also, he regarded the glandular parapodial masses as typical. Despite the fact that he did not provide more information, we regard his specimens as belonging to *N. confusa* sp. n. Other Mexican Pacific reports of *N. pelagica occidentalis* by Bastida-Zavala (1993, 1995) from nearby localities might also be conspecific.

Dean (2001) reported *N. oligohalina* from Pacific Costa Rican coasts, noticed the problems in the taxonomic history of the species, and regarded it as different from *N. oc-*

cidentalis. According to his description Costa Rican specimens differ from *N. oligohalina* in the number of paragnaths, mainly in areas I, III and IV. Also, in his specimens the longest tentacular cirri reached chaetiger 3, and the notopodial dorsal and neuropodial ventral ligules were subequal to or shorter than notopodial ventral and neuroacicular ligules throughout body, whereas in *N. oligohalina* the longest tentacular cirri reaches chaetiger 7, and their ligules are larger in midbody and posterior chaetigers. Likewise, Costa Rican specimens resemble *N. confusa* sp. n. and probably belong to the same species and this might also include the record from Cocos Island (Dean et al. 2012). Nevertheless, these records cannot be assigned to *N. oligohalina* unequivocally until specimens are evaluated.

Habitat. Holotype found on wrinkled penshell *Pinna rugosa* Sowerby, 1835, sponges and filamentous green algae; other specimens were found in sponges and green algae near the type locality. Specimens from Bahía de Los Ángeles were associated with another penshell, *Atrina maura* (Sowerby, 1835), and specimens from Estero El Yugo were found on filamentous green algae on mangrove roots. Bastida-Zavala (1995) found specimens on corals.

Distribution. Gulf of California, Eastern Pacific coasts of Mexico. Probably extends to Costa Rica, in shallow water.

Reproduction patterns and dispersal in *Nereis* species studied. Some authors have emphasized the utility of reproductive patterns in taxonomy for species discrimination in closely related taxa (Smith 1958, Clark 1977). Also, strategies for larvae survival would be relevant, especially because they determine larval transport and its dispersal potential. An interesting strategy is when only males form epitokes and females remain atokous or are barely modified, as in *Alitta virens* (Sars, 1835) and *Websterinereis glauca* (Claparède, 1870). In *A. virens*, males form epitokes but females remain atokous or present very slight changes, also females spawn into or in the opening of their burrows (Bass and Brafield 1972). In *W. glauca*, female transformation is reduced, and females produce mucous tubes to deposit and incubate their eggs, while males can swarm (Pettibone 1971).

Early studies considered that *N. garwoodi* presented a similar reproductive mode as *A. virens* or *W. glauca*, because the paralectotype female of *N. garwoodi* has a slight transformation; however, after further revision of additional material, a fully transformed female was found. We have no further details about its capacity for building mucous tubes or if females do not emerge to the water column or if gametes are retained in tubes.

In the material available of *N. oligohalina*, no completely transformed females were encountered, but perhaps with further sampling efforts they may appear. Another important consideration is the reduced size of males compared to females, even in the same sample; this has been noted for *H. diversicolor* (Bartels-Hardege and Zeeck 1990). In this case, *N. oligohalina* males can swarm while females remain inside cavities, as in *A. virens* and *W. glauca*; the fact that there are many large females filled with oocytes points toward this direction.

Reproduction modes in estuarine species play a crucial role in their dispersal because the formation of planktonic larvae can determine their distribution range. Bilton et al. (2002) proposed two life-cycle models for estuarine species that have larvae: export vs retention strategies. In the former, the adults respond to physical or biological

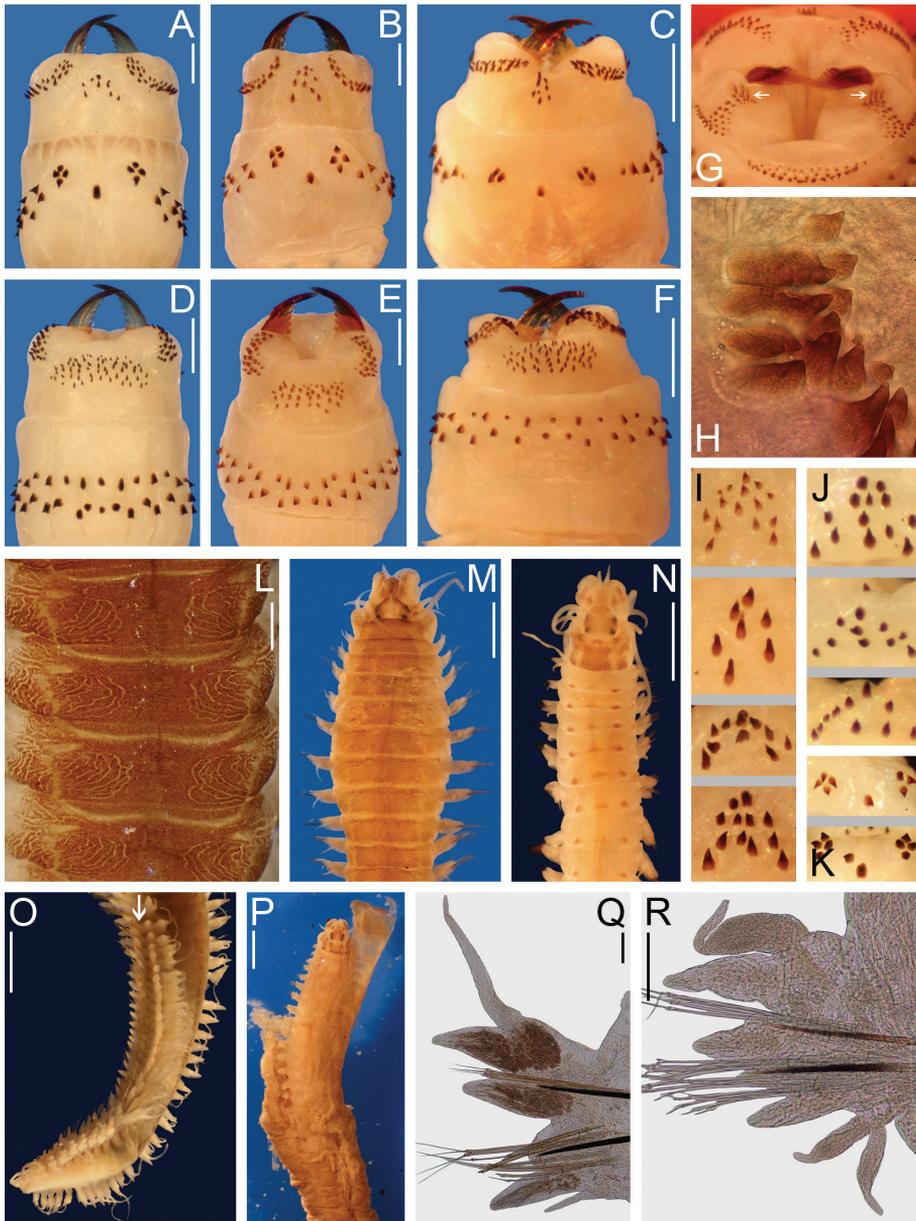


Figure 6. Variation of *Nereis* species studied. *N. oligohalina* **A, D, J-L, O, Q** from ECOSUR–OH–P0760. *N. garwoodi* **B, E** from paralectotype ECOSUR 0066; **I, M, R** from ECOSUR P2834. *N. confusa* sp. n. **C, F-H, N, P** from ECOSUR P2838. **A–C** Pharynges everted, dorsal view **D–F** Pharynges everted, ventral view **G** Pharynx everted, anterior view, showing merged paragnaths (arrows) **H** Close-up of merged paragnaths on area IV **I–J** Variations on area I **K** Variations on areas V and VI **L** Fingerprint-like pattern, dorsal view **M–N** Pigmentation patterns on anterior ends, dorsal view **O** Parapodial furrow in posterior end, lateral view (arrow indicates start) **P** Specimen on tube, dorsal view **Q** Parapodium from posterior chaetiger, anterior view **R** Ventral cirrus duplicated, chaetiger 5, anterior view. Scale bars: 0.5 mm (**A–F, L**); 1 mm (**M–P**); 0.1 mm (**Q–R**).

factors by releasing gametes or larvae in the lower estuary; larvae are driven out from the estuary, mainly by tides, and later juveniles or adults return to the estuary. In the retention strategy, adults release their gametes or larvae in the upper estuarine areas, then they undergo early development in middle estuary; there, larvae have vertical migrations during circadian ebb-flood tidal regimes such that larvae are not exported but retained within the estuary (Bilton et al. 2002).

Based on the above, we hypothesize that *N. oligohalina* has an export strategy; it could disperse thanks to surface currents running parallel to the continental margin, and this would explain its presence along Gulf of Mexico estuaries. Similarly, distribution of *N. confusa* sp. n., with mainly marine habitats, could be due to current patterns along the Gulf of California.

However, sometimes the distribution patterns cannot be explained by currents and tidal dynamics. For example, De Jesús-Flores et al. (2015) determined that *Laeonereis nota* (Treadwell, 1941), described for Galveston, Texas, is also present in Chetumal Bay; *L. nota* spawn into their burrows, limiting their dispersal by currents. The explanation for this discontinuous distribution lies in passive dispersal through migratory birds, because they use nereidids as food (De Jesús-Flores et al. 2015). Similarly *N. garwoodi* could have a classical retention strategy, but a wide, fragmented distribution caused by migratory birds.

Further considerations. The present study demonstrates the need to encourage re-descriptions of closely related and widely distributed species and, should it be necessary, the establishment of new species if there are conspicuous morphological differences.

Further, clarifying species delineation and distribution are urgent because they are essential for biogeography and phylogenetics. Reuscher and Shirley (2014) studied the distribution patterns of polychaetes from the Gulf of Mexico; a recent species list was used (Fauchald and Solís-Weiss 2009) and current taxonomy verified in WoRMS (Read and Fauchald 2015). They found that among all species recorded, 32% were cosmopolitan, 15% Pan-American and 9% Pan-Atlantic (*N. oligohalina* was regarded as Pan-American, which is incorrect as shown above). They concluded: “Most polychaete families are in need of global and regional revisions. Clear species boundaries have to be established by means of taxonomic research based on morphology and genetic analyses. Geographical ranges of species should be revised in order to eliminate false conclusions about distributions of species.”

Key to species of *Nereis* from the Grand Caribbean Region

(Modified from González-Escalante and Salazar-Vallejo 2003)

- | | | |
|------|---|---|
| 1 | Area V without paragnaths | 2 |
| – | Area V with paragnaths..... | 9 |
| 2(1) | Parapodial ligules long, slender; ceratophores distinct | |
| | <i>N. caymanensis</i> Fauchald, 1977 | |

- Parapodial ligules not enlarged; ceratophores indistinct 3
- 3(2) Notopodia with prechaetal lobes *N. goajirana* Augener, 1933¹
- Notopodia without prechaetal lobes 4
- 4(3) Dorsal cirri shorter than notopodial ligules; notopodial homogomph falcigers with oval blades *N. grayi* Pettibone, 1956
- Dorsal cirri subequal or longer than notopodial ligules; notopodial homogomph falcigers with falcate blades 5
- 5(4) Paragnaths on area I absent; notopodial homogomph falcigers with bifid blade *N. panamensis* Fauchald, 1977
- Paragnaths on area I present, notopodial homogomph falcigers with entire blade 6
- 6(5) Area VII-VIII with few paragnaths, usually 5–7 7
- Area VII-VIII with numerous paragnaths, more than 40 8
- 7(6) Longest tentacular cirri reaching chaetiger 7; area VI usually with 9 paragnaths *N. riisei* (Grube & Ørsted in Grube, 1858)²
- Longest tentacular cirri reaching chaetiger 4; area VI usually with 3 paragnaths *N. allenae* Pettibone, 1956³
- 8(6) Notopodial homogomph falciger with numerous teeth, distal tooth recurved, one quarter of blade embedded in shaft *N. occidentalis* Hartman, 1945
- Notopodial homogomph falciger with few teeth, without distal tooth, one-half of blade embedded in shaft *N. pelagica* Linnaeus, 1758⁴
- 9(1) Notopodial homogomph falcigers with cutting edge smooth *N. largoensis* Treadwell, 1931⁵
- Notopodial homogomph falcigers with cutting edge denticulate 10
- 10(9) Dorsal pigmentation as a striated pattern, usually along first 10 chaetigers; tentacular cirri reaching beyond chaetiger 7 11
- Dorsal pigmentation different; tentacular cirri reaching up to chaetiger 7 12
- 11(10) Area I with paragnaths in an oval; longest tentacular cirri reaching up to chaetiger 9 *N. rigida* Grube & Ørsted in Grube, 1858⁶
- Area I with paragnaths in a triangle; longest tentacular cirri reaching up to chaetiger 12 *N. garwoodi* González-Escalante & Salazar-Vallejo, 2003
- 12(10) Dorsal pigmentation with fingerprint-like pattern from chaetigers 10–11; notopodial ligules enlarged in posterior chaetigers *N. oligohalina* (Rioja, 1946)
- Dorsal pigmentation with spotted pattern; notopodial ligules with similar proportions along body *N. confusa* sp. n.⁷

¹ This species has not been found recently (Báez and Ardila 2003).

² It has a doubtful amphiamerican status and there is no recent redescription. Here, descriptions by Renaud (1956) with specimens from Miami, and by Hoagland (1919) for *N. glandulata* from Porto Rico, were used. Hartman (1956) considered *N. glandulata* as a junior synonym of *N. arroyensis* Treadwell, 1901, but they differ in number of paragnaths on area VII-VIII.

- ³ De León-González et al. (1999) detailed the arrangement of paragnath number of *N. allenae* Pettibone, 1956.
- ⁴ After Chambers and Garwood (1992).
- ⁵ In the original description of *N. largoensis* as *N. brevicirrata*, Treadwell (1929) reported area V without paragnaths and homogomph falciger with lenticular blades. However, Hartman (1956) found one paragnath on area V and homogomph falciger six times longer than wide.
- ⁶ Augener (1906) introduced the species name for the Caribbean fauna; however, Grube (1858) used a single specimen from Pacific Costa Rica (Puntarenas). Here the original description by Grube was used, and it was included as a contrast for *N. confusa* sp. n.
- ⁷ Distributed in the Mexican Pacific, often confused with *N. oligohalina*.

Additional comments. Several species recorded from the Grand Caribbean are questionable, such as *N. falcaria* (Willey, 1905), *N. jacksoni* Kinberg, 1866, *N. victoriana* Augener, 1918, *N. falsa* de Quatrefages, 1865, *N. callaona* (Grube, 1857) and *N. lamellosa* Ehlers, 1868; consequently, they were not included in the key because their type localities are distant and different from the tropical American conditions. Only *N. pelagica* was included in order to contrast it with *N. occidentalis*, but its records from the Grand Caribbean Sea might belong to a different species.

Acknowledgements

We thank María A. Tovar-Hernández, Jesús. Á. de León-González (UANL), and Tulio F. Villalobos-Guerrero, for making available some of the material of *N. oligohalina* than made this study possible. We also thank Astrid E. Te-Gómez and Concepción Licona-Rosado help during fieldwork, and Luis F. Carrera-Parra by offering helpful suggestions about type-materials. This publication is part of the requirements for obtaining a M.S. degree at El Colegio de la Frontera Sur, Unidad Chetumal (ECOSUR), and supplied by a fellowship from CONACyT.

References

- Amaral ACZ, Nallin SAH, Steiner TM, Forroni T de O, Filho DG (2012) Catálogo das espécies de Annelida Polychaeta do Brasil. http://www.ib.unicamp.br/museu_zoologia/sites/www.ib.unicamp.br/museu_zoologia/files/Cat%C3%A1logo_Polychaeta_Brasil_Amaral_et_al_2013_1a.pdf [2013-03-06]
- Augener H (1906) Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico and the Caribbean Sea, and on the east coast of the United States, 1877 to 1880, by the U.S.S. Coast Survey Steamer “Blake,” Lieut. Commander C.D. Sigsbee,

- U.S.N., and the commander J.R. Bartlett, U.S.N., commanding. XLII. Westindische Polychaeten. Bulletin of the Museum of Comparative Zoology 43(4): 91–196.
- Báez DP, Ardila NE (2003) Poliquetos (Annelida: Polychaeta) del Mar Caribe colombiano. Biota Colombiana 4: 89–109.
- Bakken T (2007) Revision of *Pseudonereis* (Polychaeta, Nereididae). Zoological Journal of the Linnean Society 150: 145–176. doi: 10.1111/j.1096-3642.2007.00289.x
- Bakken T, Glasby CJ, Wilson RS (2009) A review of paragnath morphology in Nereididae (Polychaeta). Zoosymposia 2: 305–316.
- Bakken T, Wilson RS (2005) Phylogeny of nereidids (Polychaeta, Nereididae) with paragnaths. Zoologica Scripta 34: 507–547. doi: 10.1111/j.1463-6409.2005.00200.x
- Bartels-Hardege H, Zeeck E (1990) Reproductive behavior of *Nereis diversicolor* (Annelida: Polychaeta). Marine Biology 106: 409–412. doi: 10.1007/BF01344320
- Bass NR, Brafield AE (1972) The life-cycle of the polychaete *Nereis virens*. Journal of the Marine Biological Association of the United Kingdom 52: 701–726. doi: 10.1017/S0025315400021664
- Bastida-Zavala JR (1993) Taxonomía y Composición Biogeográfica de los Poliquetos (Annelida: Polychaeta) de la Bahía de la Paz, B.C.S., México. Revista de Investigación Científica UABCS 4: 11–39.
- Bastida-Zavala JR (1995) Poliquetos (Annelida: Polychaeta) del Arrecife Coralino de Cabo Pulmo-Los Frailes, B.C.S., México. Revista de Zoología 6: 9–29.
- Berkeley E, Berkeley C (1958) Some notes on a collection of polychaeta from the Northeast Pacific south of latitude 32° N. Canadian Journal of Zoology 36: 399–407. doi: 10.1139/z58-034
- Berkeley E, Berkeley C (1960) Notes on some Polychaeta from the West Coast of Mexico, Panama, and California. Canadian Journal of Zoology 38: 357–362. doi: 10.1139/z60-040
- Bilton DT, Paula J, Bishop JDD (2002) Dispersal, genetic differentiation and speciation in estuarine organisms. Estuarine, Coastal and Shelf Science 55: 937–952. doi: 10.1006/ecss.2002.1037
- Boilly-Marer Y (1972) Sur la signification et le déterminisme des caracteres sexuels somatiques chez les Nereidae (Annélides polychètes). Archives de Zoologie Expérimentale et Générale 113: 369–393.
- Carrillo L, Palacios-Hernández E, Ramírez AM, Morales-Vela JB (2009) Características hidrometeorológicas y batimétricas. In: Espinosa-Ávalos J, Islebe GA, Hernández-Arana HA (Eds) El Sistema ecológico de la bahía de Chetumal/Corozal: costa occidental del Mar Caribe. ECOSUR, Chetumal, México, 12–20.
- Chambers S, Garwood P (1992) Polychaetes from Scottish Waters. A Guide to Identification, 3. Family Nereidae. National Museum, Edinburgh, 65 pp.
- Charrier H (1920) Recherches sur la "*Nereis fucata*" Sav. Actes de la Société Linnéenne de Bordeaux 72: 5–144.
- Clark RB (1977) Reproduction, speciation and polychaete taxonomy. In: Reish DJ, Fauchald K (Eds) Essays on the Polychaetous Annelids in Memory of Dr. Olga Hartman. Allan Hancock Foundation, University of South California, Los Angeles, 477–501.

- Darbyshire T (2014) Intertidal and nearshore Nereididae (Annelida) of the Falkland Islands, southwestern Atlantic, including a new species of *Gymnonereis*. Zookeys 427: 75–108. doi: 10.3897/zookeys.427.7296
- Day JH (1973) New Polychaeta from Beaufort, with a key to all species recorded from North Carolina. NOAA Technical Report NMFS CIRC-375: 1–153. doi: 10.5962/bhl.title.62852
- De Jesús-Flores C, Salazar-González SA, Salazar-Vallejo SI (2015) Morphological distinction between estuarine nereidid polychaetes: *Laeonereis culveri* (Webster, 1879) and *L. nota* (Treadwell, 1941). Revista de Biología Tropical (sent for evaluation: Mar. 2015).
- De León-González JÁ, Solís-Weiss V, Ochoa-Rivera V (1999) Nereidids (Polychaeta) from the Caribbean Sea and adjacent coral islands of the southern Gulf of Mexico. Proceedings of the Biological Society of Washington 112: 667–681.
- Dean HK (2001) Some Nereididae (Annelida: Polychaeta) from the Pacific Coast of Costa Rica. Revista de Biología Tropical 40: 37–67.
- Dean HK, Sibaja-Cordero JA, Cortés J (2012) Polychaetes (Annelida: Polychaeta) of Cocos Island National Park, Pacific Costa Rica. Pacific Science 66: 347–386. doi: 10.2984/66.3.8
- Evenhuis NL (2008) A compendium of zoological type nomenclature: A reference source. Bishop Museum Technical Report 41: 1–25.
- Fauchald K (1977) The polychaete worms: Definitions and keys to the orders, families and genera. Natural History Museum of Los Angeles County, Science Series 28: 1–190.
- Fauchald K, Solís-Weiss V (2009) Polychaeta (Annelida) of the Gulf of Mexico. In: Felder DL, Camp DK (Eds) Gulf of Mexico origin, waters and Biota: volume I, biodiversity. Texas A&M University Press, College Station, 751–788.
- Fauvel P (1923) Polychètes Errantes. Faune de France 5: 1–488.
- Glasby CJ (1999) The Namanereidinae (Polychaeta: Nereididae). 1. Taxonomy and Phylogeny. Records of the Australian Museum, Supplement 25: 1–129. doi: 10.3853/j.0812-7387.25.1999.1354
- Glasby CJ, Timm T, Muir AI (2009) Catalogue of non-marine Polychaeta (Annelida) of the World. Zootaxa 2070: 1–52.
- Glasby CJ, Wilson RS, Bakken T (2011) Redescription of the Indo-Pacific polychaete *Neanthes pachychaeta* (Fauvel, 1918) n. comb. (Annelida, Phyllodocida, Nereididae) and its synonyms. Zoosystema 33(3): 361–375. doi: 10.5252/z2011n3a5
- Glasby CJ, Wei N-WV, Gibb KS (2013) Cryptic species of Nereididae (Annelida: Polychaeta) on Australian coral reefs. Invertebrate Systematics 27: 245–264. doi: 10.1071/IS12031
- González-Escalante LE, Salazar-Vallejo SI (2003) A new estuarine species, *Nereis garwoodi* (Polychaeta: Nereididae), from Bahía Chetumal, Mexican Caribbean coast. Revista de Biología Tropical 51: 155–164.
- Grube AE (1858) Annulata örstediana. Enumeratio Annulorum, quae in itinere per Indiam occidentalem et Americam centralem annis 1845-1848 suscepto legit cl. A.S. Örsted, adjectis speciebus nonnullis a cl. H. Kröyero in itinere ad Americam meridionalem collectis, (Fortsæ). Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening for 1857: 158–186.
- Hartman O (1948) The marine annelids erected by Kinberg with notes on some others types in the Swedish State Museum. Arkiv för Zoologi 42A(1): 1–156.

- Hartman O (1951) The littoral marine annelids of the Gulf of Mexico. Publications of the Institute of Marine Science 2: 7–124.
- Hartman O (1954) Polychaetous annelids of the Gulf of Mexico. In: Galtsoff PS (Ed.) Gulf of Mexico. Its Origin, Waters, and Marine Life. Fishery Bulletin of the Fish and Wildlife Service. Volume 55, 413–417.
- Hartman O (1956) Polychaetous annelids erected by Treadwell, 1891 to 1948, together with a brief chronology. Bulletin of the American Museum of Natural History 109: 239–310.
- Herpin R (1925) Recherches biologiques sur la reproduction et le développement de quelques annélides polychètes. Bulletin de la Société des Sciences Naturelles de l'Ouest de la France, série 4ème, 5: 1–250.
- Hoagland RA (1919) Polychaetous annelids from Porto Rico, the Florida Keys, and Bermuda. Bulletin of the American Museum of Natural History 41: 571–591.
- ICZN (1999) International Code of Zoological Nomenclature, 4th ed. International Trust for Zoological Nomenclature (The Natural History Museum), London.
- Lana P da C, Santos CSG, Garraffoni ARS, Oliveira VM, Radashevsky V (2006) Checklist of Polychaete Species from Paraná State (Southern Brazil). Check List 2: 30–63. doi: 10.15560/2.3.30
- Lara-Domínguez AL, Contreras-Espinosa F, Castañeda-López O, Barba-Macías E, Pérez-Hernández MA (2011) Lagunas costeras y estuarios. In: La biodiversidad en Veracruz: Estudio de caso. Comisión para el Conocimiento y Uso de la Biodiversidad (CONABIO), Gobierno del Estado de Veracruz, Universidad Veracruzana (UV), Instituto de Ecología A.C. (INECOL), 301–317.
- Linnaeus C (1758) Systema Naturae per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. 10th Ed., Laurentii Salvii, Holmie (Stockholm), 823 pp.
- Liñero-Arana I, Díaz-Díaz Ó (2007) Nuevas adiciones de Nereididae (Annelida: Polychaeta) para las costas de Venezuela. Boletín del Instituto Oceanográfico de Venezuela 46: 149–159.
- Oliveira VM, Santos CSG, Lana P da C, Camargo MG (2010) Morphological variations caused by fixation techniques may lead to taxonomic confusion in *Laeonereis* (Polychaeta: Nereididae). Zoologia (Curitiba) 27: 146–150. doi: 10.1590/S1984-46702010000100022
- Pettibone MH (1956) Some polychaete worms of the families Hesionidae, Syllidae, and Nereidae from the east coast of North America, West Indies, and Gulf of Mexico. Journal of the Washington Academy of Sciences 46: 281–294.
- Pettibone MH (1971) Revision of some species referred to *Leptonereis*, *Nicon*, and *Laeonereis* (Polychaeta: Nereididae). Smithsonian contribution to Zoology 104: 1–53. doi: 10.5479/si.00810282.104
- Read GB (1980) A new species of *Nereis* (Polychaeta: Nereididae) from Wellington, New Zealand, Rock Shores. Journal of the Royal Society of New Zealand 10: 185–193. doi: 10.1080/03036758.1980.10427174
- Read GB (2007) Taxonomy of sympatric New Zealand species of *Platynereis*, with description of three new species additional to *P. australis* (Schmarda) (Annelida: Polychaeta: Nereididae). Zootaxa 1558: 1–28.

- Read G, Fauchald K (Eds) (2015) World Polychaeta database. <http://www.marinespecies.org/polychaeta> [2015-05-26]
- Renaud JC (1956) A report of some polychaetous annelids from the Miami-Bimini area. *American Museum Novitates* 1812: 1–40.
- Reuscher MG, Shirley TC (2014) Diversity, distribution, and zoogeography of benthic polychaetes in the Gulf of Mexico. *Marine Biodiversity*, 1–14. doi: 10.1007/s12526-014-0222-7
- Rioja E (1946) Estudios anelidológicos. 15. Nereidos de agua salobre de los esteros del litoral del Golfo de México. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México* 17: 205–214.
- Rioja E (1947) Estudios anelidológicos. 19. Observaciones sobre algunos nereidos de las costas de México. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México* 28: 247–266.
- Rioja E (1960) Estudios anelidológicos. 24. Adiciones a la fauna de anélidos poliquetos de las costas orientales de México. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México* 31: 289–316.
- Rioja E (1962) Estudios anelidológicos. 26. Algunos anélidos poliquetos de las costas del Pacífico de México. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México* 33: 131–229.
- Ruiz M, López-Portillo J (2014) Variación espacio-temporal de la comunidad de macroinvertebrados epibiontes en las raíces del mangle rojo *Rhizophora mangle* (Rhizophoraceae) en la laguna costera de La Mancha, Veracruz, México. *Revista de Biología Tropical* 62: 1309–1330. doi: 10.15517/rbt.v62i4.12582
- Ruiz-Guerrero M, López-Portillo Guzmán J (2006) Los invertebrados. In: Moreno-Casasola P (Ed.) *Entornos Veracruzanos: La Costa de La Mancha*. Instituto de Ecología, Xalapa, 341–361.
- Salazar-Vallejo SI (1989) Enrique Rioja y su contribución al estudio de los poliquetos (Anelida: Polychaeta) en México. *Brenesia* 30: 39–65.
- Salazar-Vallejo SI (2011) Revision of *Piromis* Kinberg, 1867 and *Pycnoderma* Grube, 1877 (Polychaeta: Flabelligeridae). *Zootaxa* 2819: 1–50.
- Santos CSG, Lana P da C (2003) Nereididae (Polychaeta) da costa Nordeste do Brasil, 3 Gêneros *Ceratonereis* e *Nereis*. *Iheringia, Série Zoologia* 93: 5–22.
- Santos CSG, Pleijel F, Lana P da C, Rouse GW (2005) Phylogenetic relationships within Nereididae (Annelida: Polychaeta). *Invertebrate Systematics* 19: 557–576. doi: 10.1071/IS05001
- Sendall K, Salazar-Vallejo SI (2013) Revision of *Sternaspis* Otto, 1821 (Polychaeta, Sternaspidae). *Zookeys* 286: 1–74. doi: 10.3897/zookeys.286.4438
- Smith RI (1958) On reproductive pattern as a specific characteristic among nereid polychaetes. *Systematic Zoology* 7: 60–73. doi: 10.2307/2411793
- Treadwell AL (1929) New species of polychaetous annelids in the collections of the American Museum of Natural History, from Porto Rico, Florida, Lower California, and British Somaliland. *American Museum Novitates* 392: 1–13.
- Villalobos-Guerrero TF, Carrera-Parra LF (2015) Redescription of *Alitta succinea* (Leuckart, 1847) and reinstatement of *A. acutifolia* (Ehlers, 1901) n. comb. based upon morphologi-

cal and molecular data (Polychaeta: Nereididae). *Zootaxa* 3919: 157–178. doi: 10.11646/zootaxa.3919.1.7

Yáñez-Rivera B, Carrera-Parra LF (2012) Reestablishment of *Notopygos megalops* McIntosh, description of *N. caribea* sp. n. from the Greater Caribbean and barcoding of “amphiamerican” *Notopygos* species (Annelida, Amphinomidae). *Zookeys* 223: 69–84. doi: 10.3897/zookeys.223.3561

Leucothoe eltoni sp. n., a new species of commensal leucothoid amphipod from coral reefs in Raja Ampat, Indonesia (Crustacea, Amphipoda)

James Darwin Thomas¹

¹ Reef Foundation Inc., Dania, Florida, USA

Corresponding author: James Darwin Thomas (anamixis@hotmail.com)

Academic editor: Alan Myers | Received 5 February 2015 | Accepted 12 August 2015 | Published 25 August 2015

<http://zoobank.org/ED62E75F-5514-4DA9-A71F-4DB8E8A9DAA1>

Citation: Thomas JD (2015) *Leucothoe eltoni* sp. n., a new species of commensal leucothoid amphipod from coral reefs in Raja Ampat, Indonesia (Crustacea, Amphipoda). ZooKeys 518: 51–66. doi: 10.3897/zookeys.518.9340

Abstract

A new species of leucothoid amphipod, *Leucothoe eltoni* sp. n., is described from coral reefs in Raja Ampat, Indonesia where it inhabits the branchial chambers of solitary tunicates. With an inflated first gnathopod superficially resembling the genus *Paraleucothoe*, this new species has a two-articulate maxilla 1 palp characteristic of the genus *Leucothoe*. While described from coral reef environments in tropical Indonesia and the Philippines, it is an established invasive species in the Hawaiian Islands. The most likely mode of introduction was a US Navy dry dock transported to Pearl Harbor in 1992 from Subic Bay, Philippines.

Keywords

Amphipods, coral reefs, ascidians, sponges, invasive species, model organisms, taxonomy

Introduction

While leucothoid amphipods are frequently encountered in marine faunal surveys and inventories information about their invertebrate hosts is rarely known and infrequently documented. The Leucothoidae, once thought to be a cosmopolitan and widespread taxon are now known to be a highly habitat-specific species complex. Taxonomic clarity within the group has been hampered by widespread and incorrect records of *Leucothoe spinicarpa* (Abildgaard, 1789). Upon further analysis many of these records are

now proving to be discrete species, thus diminishing the cosmopolitan concept within the group (Krapp-Schickell and De Broyer 2014).

Because leucothoids lack a dispersive larval stage and frequently inhabit internal chambers of sessile invertebrate hosts they are potentially informative proxies for evolutionary diversity. Recent developments within the taxonomy of the Leucothoidae include: (1) availability of an electronic taxonomic database (Thomas and White 2014); and (2) widely deployed specialized *in-situ* underwater collecting methodologies. Specialized collection methods that isolate hosts and commensals together (sponges, ascidians, and bivalve mollusks) has led to re-examination of existing collections and spurred new efforts resulting in an increase in recently described leucothoid taxa for study and research (Myers 2013, Krapp-Schickel and DeBroyer 2014, Ortiz and Winfield 2012, Thomas 1979, 1997a,b, Thomas and Klebba 2006, 2007, Thomas and Krapp-Schickel 2011, Thomas and Taylor 1981, White and Thomas 2009, White and Reimer 2012a, 2012b, 2012c, Winfield and Alvarez 2009, Winfield et al. 2009) including new approaches for molecular analysis (White 2010, 2011a,b, White and Reimer 2012d).

With their distinct morphology and common occurrence in shallow coastal marine environments, leucothoid amphipods drew the attention of early naturalists, resulting in some of the earliest recorded amphipod descriptions. While important taxonomic records, these early descriptions were often inadequately illustrated and described contributing to subsequent taxonomic confusion in the group. With increasing concerns about global climate change and loss of marine biodiversity, leucothoid amphipods are sensitive model organisms highly susceptible to a variety of toxicants and pollutants (Reish and Barnard 1969) and capable of providing a comparative diversity framework and serving as measures of change in marine ecosystems (Thomas 1993, 1997b). While the lack a larval stage limits widespread dispersal, some tube-dwelling and fouling community amphipods attain broad distributions as drifters on seaweed and algae, attached to floating debris, as components of fouling communities, and their occurrence in ballast water (Carlton 2010). Leucothoids, with their constrained distributions and commensal life history, can serve as valid indicators of environmental change and sentinels of lineage-based evolutionary history (Thomas 1997a). The use of leucothoids in such context depends on precise taxonomies and representative collections across broad marine habitats. This increased precision in determining composition and assessing threat levels is of interest especially for increasingly impacted coral reef systems (Thomas 1993, 1997b). Assessments incorporating cryptic biota could provide more refined and detailed insights than traditional coral reef inventories that incorporate organisms with large-scale dispersal capabilities (Hoeksema 2007).

Currently the revised Leucothoidae (*sensu stricto*) comprises 176 species in five genera. This includes 42 former anamixid species in *Anamixis* Stebbing, 1897 (23 spp.); *Nepanamixis* Thomas, 1997 (4 spp.); and *Paranamixis* Schellenberg, 1938 (15 spp.); and 134 leucothoid species comprised of *Leucothoe* Leach (132 spp.), and *Paraleucothoe* Stebbing, 1899 (2 spp.). Species in the former anamixid genera differ from other leucothoids in exhibiting radical sexual dimorphism, eusocial and harem

guarding population structure, and tropic to warm temperate distributions. Species in *Leucothoe* and *Paraleucothoe* exhibit minor to moderate sexual dimorphism, and have tropic to polar distributions. Recent 18S rDNA sequence data by White and Reimer (2012d) suggest that the generic boundaries and definition of *Paraleucothoe* should be evaluated in the light of new molecular and morphological data.

Materials and methods

Using SCUBA and specialized underwater collecting techniques amphipods were sampled *in-situ* from ascidians, sponges, and bivalves throughout Raja Ampat, Indonesia. Specimens were captured *in-situ* directly from their host either with a modified squirt bottle or by isolating hosts and substrata underwater in plastic bags and later coercing the amphipods from the host using a small amount of freshwater or formalin in the lab.

Specimens were either fixed in 2% buffered formalin or 70% ethanol. Prior to observation, specimens were gently cleaned with small sable hair brushes, and transferred to glycerin for dissection, illustration, and analysis. For SEM analysis, specimens were rehydrated to distilled water (three fluid changes for 10 minutes each), soaked in a dilute surfactant for 15 minutes (two drops of Tween 80 in 100 ml of water), briefly sonicated (10 seconds) to remove accumulated surface debris, and re-rinsed in distilled water (three fluid changes for 10 minutes each). This preparation protocol was modified from Felgenhauer (1987) by using a more finely graded alcohol series (5%, 10%, 15%, 25%, 35%, 50%, 60%, 70%, 75%, 80%, 85%, 90%, 95%, and 100%) to prevent distortion and shrinkage. Specimens were then fixed in salt water buffered osmium tetroxide (equal parts, under fume hood) for 2.5 hours, dehydrated in a graded alcohol series, transferred to acetone (three fluid changes for 10 minutes each), soaked in Hexamethyldisilazane Reagent (HMDS) for 15 minutes, air-dried overnight, and sputter coated with palladium for scanning electron microscopy. Photographs were taken with an ISI-DS-130 dual state scanning electron microscope.

Results

Figure Legend – Capital letters in figures refer to the following appendages: **A** = antennae, **Cx** = coxae, **E** = epimera, **Hd** = head, **LL** = lower lip, **Md** = mandible, **N** = gnathopod, **P** = pereopod, **T** = telson, **U** = uropod, **UL** = upper lip, **X** = maxillae.

Capital letters to the right of each caption refer to the following: **L** = left, **R** = right. Lower case letters to the left of capital letters refer to the following adjectives: **l** = lateral, **m** = medial, **x** = magnified. Numbers to the right of capital letters refer to specific structures. “LW” in text refers to length/width ratios. Sexes are indicated by ♂ and ♀ symbols.

Material is deposited at the National Museum of Natural History, Leiden (RMNH) and at the Zoological Museum of Bogor (MZB) Indonesian Institute of

Sciences (LIPI). Additional material examined from the Bernice P. Bishop Museum (BPBM), Oahu, Hawaii, and the California Academy of Science, San Francisco, California (CASIZ).

***Leucothoe eltoni* sp. n.**

<http://zoobank.org/9C928A8A-EAC1-47E5-9A08-94AD9CC2D116>

Figures 1–9

Paraleucothoe flindersi Stebbing, 1888, Muir 1997, pp 51–52

Type locality. Reef slope, Yenweres Bay, Raja Ampat, Indonesia, 00° 29.216'S; 130° 40.394'E, coral reef slope, 20m.

Type material. Holotype. Male A, 8.10mm; MZB Cru Amp 003, 10 December 2007, Yenweres Bay, Raja Ampat, Indonesia, 00°29.216'S; 130°40.394'E, JDT-RajAM-46, 20m, collected *in-situ* from branchial baskets of *Herdmania* sp. tunicates, James Thomas, collector.

Paratypes. Female B, 7.35mm; male C, 7.40mm; and six additional specimens. RMNH.Crus.A.5055, 10 December 2007, Station number JDT-RajAM-46, 20m, collected *in-situ* from branchial baskets of *Herdmania* sp. tunicates, James Thomas, collector.

Additional material examined. Male and female specimens, RMNH.Crus.A.5056, 4 December 2004, Bunaken, Sulawesi, Indonesia, 1°37.063' N; 124°46.966' E. Station Indo04-01c, 8.5 m, from *Herdmania* sp. tunicates, reef wall in front of Living Colors Dive Resort. J. Thomas, K. White collectors. BPBM S11292-293, Pearl Harbor, Oahu, Hawaii, Station 6, 16 April 1996, from the sponge *Mycale grandis*, USN drydock "Machinist". CASIZ 204559, Philippines, Batangas Province, Maricaban Island, Cemetery Beach, 13°41.063N; 120°49.813E, coral rubble, 5 m., from *Polycarpa* tunicate, J. Thomas, collector.

Etymology. The specific epithet, *eltoni*, in honor of the rock musician Sir Elton John. Specifically, in reference to the large shoe-like first gnathopod of this species and the oversize boots Elton John wore as the local pinball champion in the movie "Tommy" (1975).

Diagnosis. Male holotype A. Antenna 1 and 2 short, less than 0.10 body length; maxilliped, inner margin of outer plate crenulate, palp 2-articulate; gnathopod 1, carpus and propodus greatly enlarged; carpus setose posteriorly; distal margin of propodus tumid, inflated; gnathopod 2, palm oblique with 3 concavities separated by truncate projections; pereopods 5-7, article 4 extending beyond 0.5× of article 5.

Description of male holotype A. Ratios of antenna 1 and 2, 0.10 and 0.09 body length; relative lengths of antenna 1 and 2, 1.00:0.89, flagellae 8 and 6-segmented. Anterior margin of head broadly truncate; mid-ventral keel produced, anterior margin produced dorsally as small knob, tapering posteriorly, ventral margin straight.

Coxae. Coxae 1-4 width ratios, 1.00:1.87:1.37:1.40, coxa 4 posterior margin widest mid posteriorly, tapering proximally, coxa 5-6 bilobed; coxa 7 reduced, ovate.

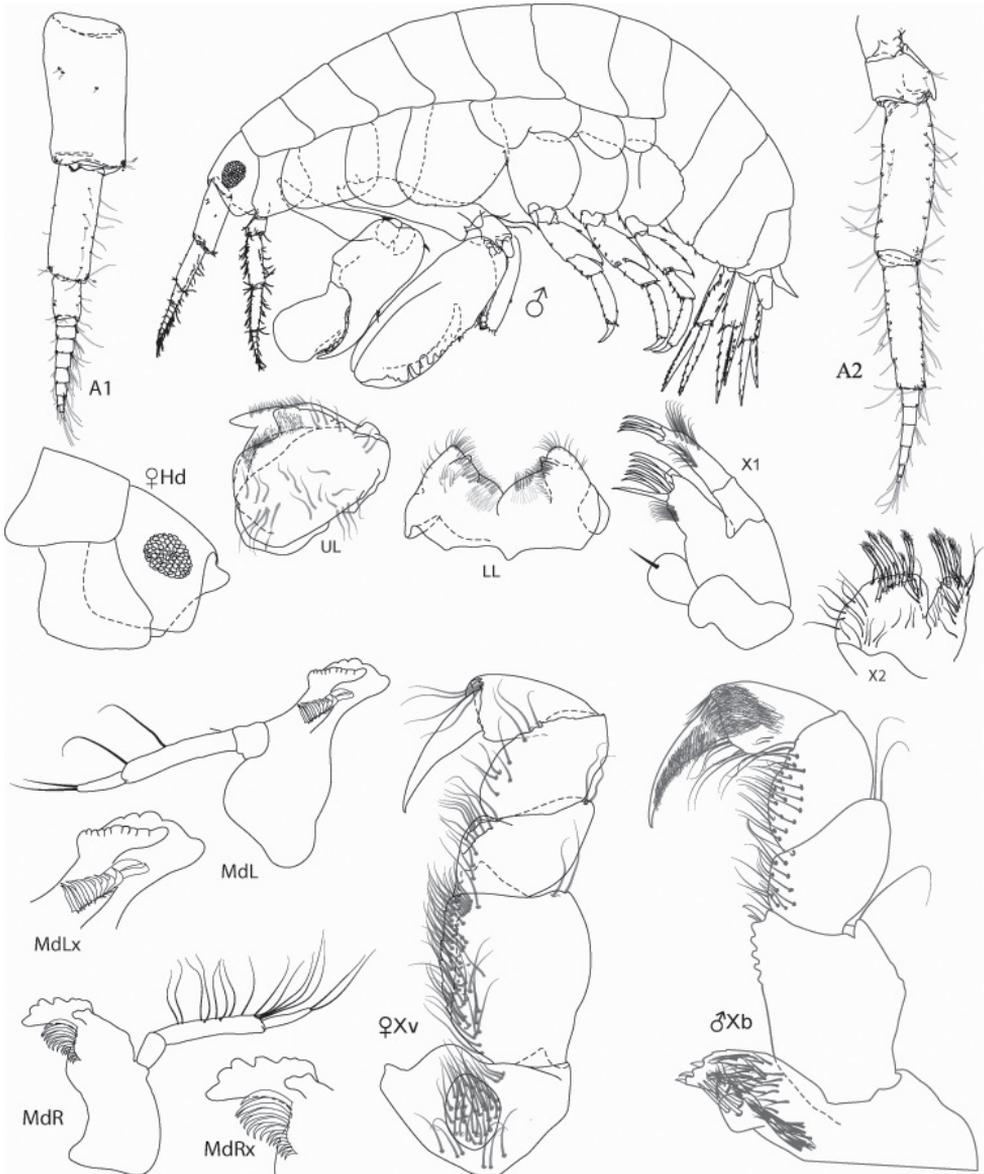


Figure 1. *Leucothoe eltoni* sp. n., holotype ♂A, 8.10 mm; paratype ♀B, 7.35 mm.

Upper lip. Asymmetrically lobate, anterior margin setose.

Mandibles. Both lacking molars; palp 3-articulate, ratio of articles 1-3 1.00:2.50:2.60; incisors moderately dentate. Left mandible, palp articles 2-3 with 2 anterior and 2 apical setae; lacinia mobilis large, strongly toothed; 13 raker spines, two distal raker spines enlarged and modified. Right mandible, palp articles 2-3 with 13 anterior and 2 apical setae; lacinia mobilis an elongated flake; 15 raker spines.

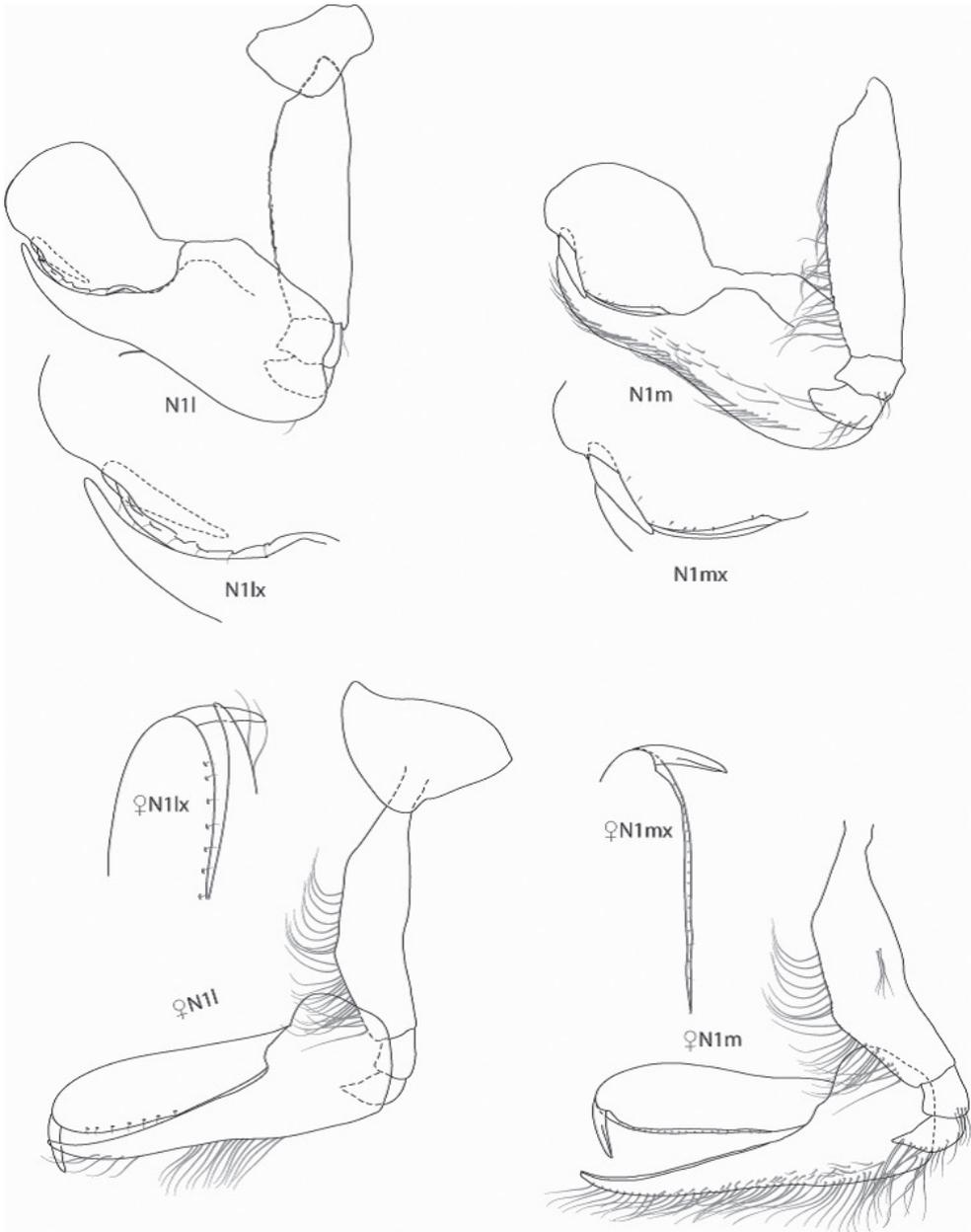


Figure 2. *Leucothoe eltoni* sp. n., gnathopod 1 lateral and medial; holotype ♂A, 8.10 mm; paratype ♀B, 7.35 mm.

Maxillae. 1, palp 2-articulate with four apical setae, and two rows nine and eleven facial setae; outer plate with seven apical setae and nine facial setae; inner plate small, ovate, with single apical seta. Maxilla 2: inner plate, distal margin with 6 apical

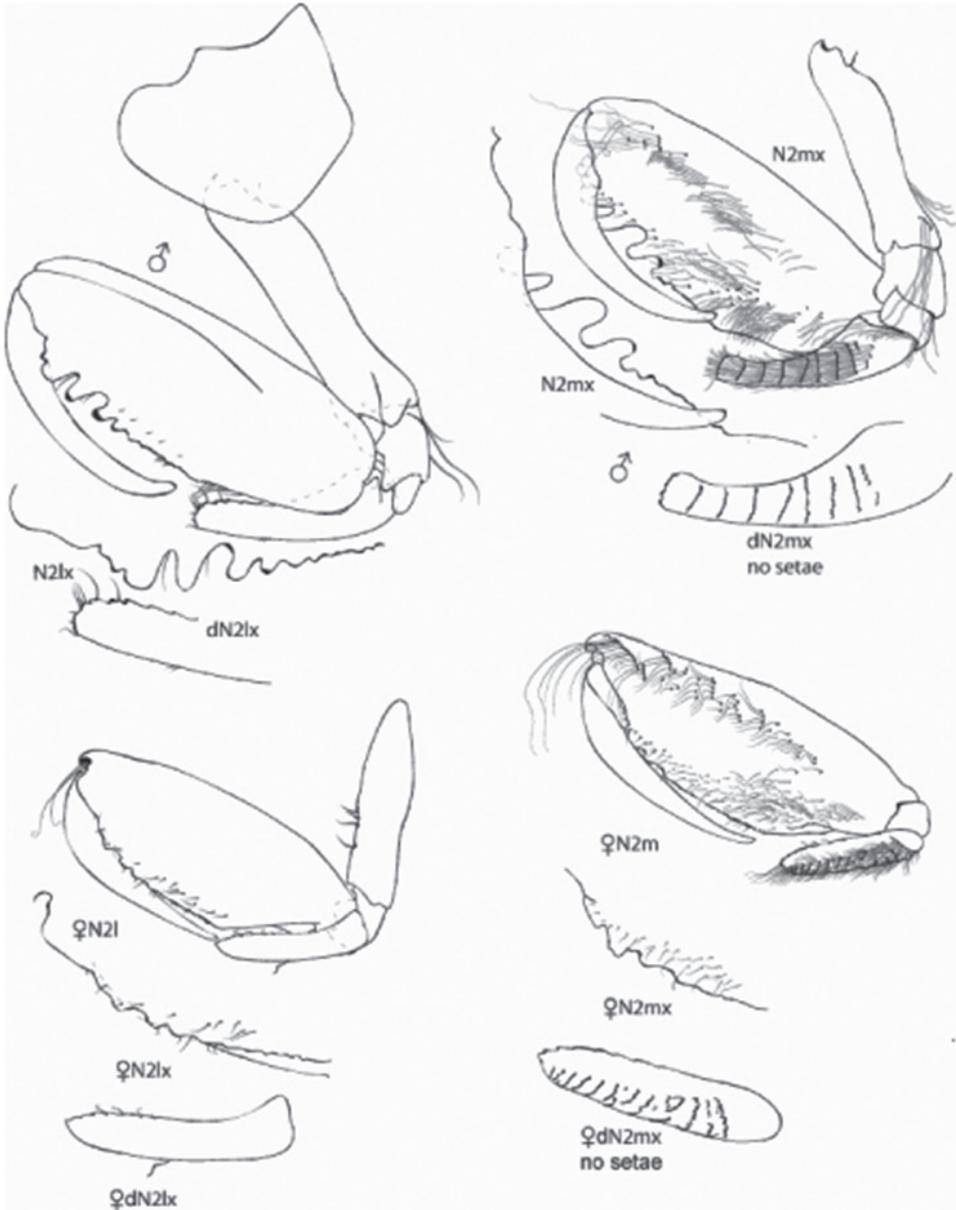


Figure 3. *Leucothoe eltoni* sp. n., gnathopod 2 medial and lateral; holotype ♂A, 8.10 mm; paratype ♀B, 7.35 mm.

setae and 6 submarginal setae, 20+ facial setae; outer plate with 5 marginal medial setae and 19 facial setae.

Maxilliped. Inner and outer plates reduced; inner plates fused, with three stout apical setae and numerous fine facial setae; outer plate, anterior one third of medi-

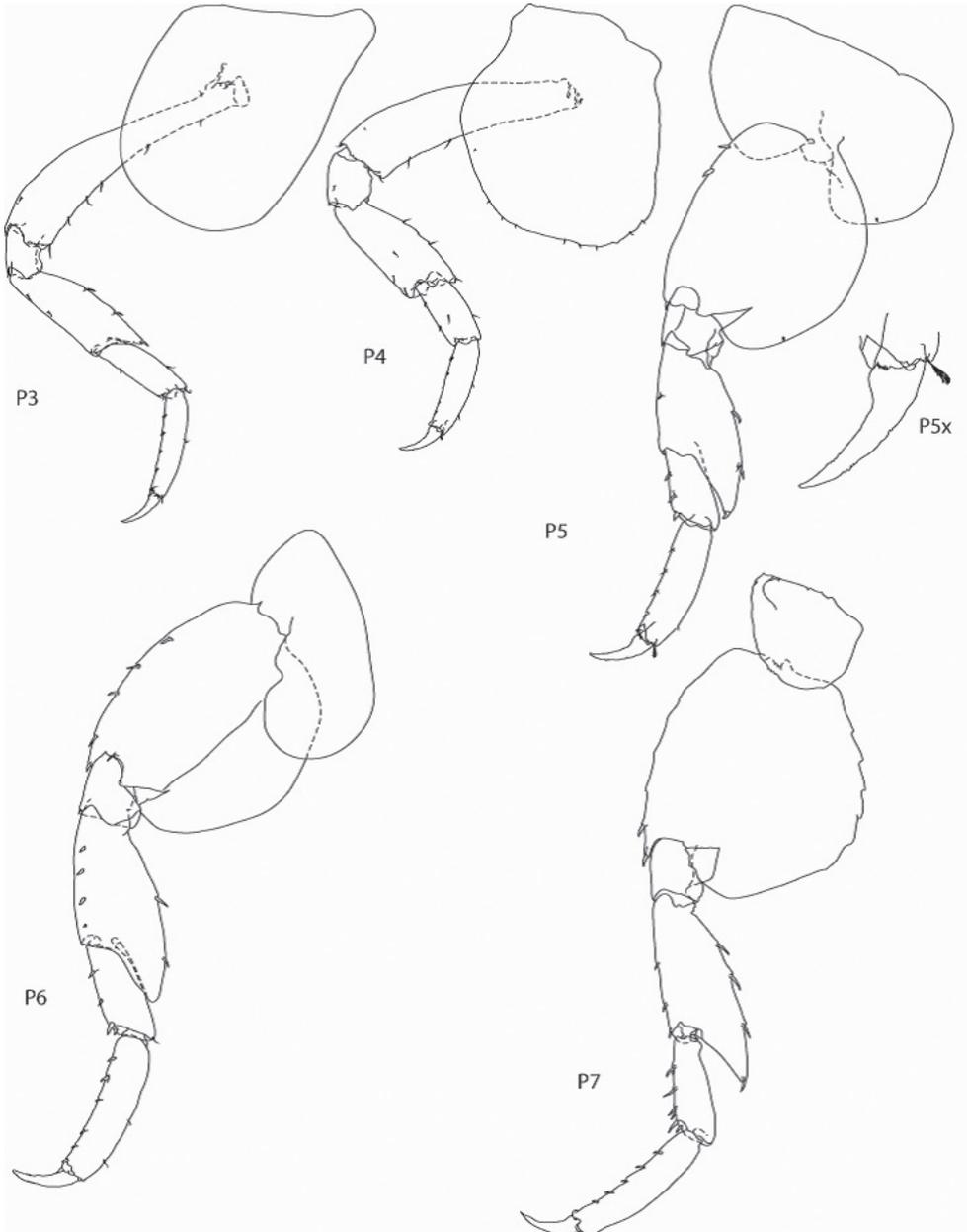


Figure 4. *Leucothoe eltoni* sp. n., holotype ♂A, 8.10 mm; pereopods 3-7.

al margin tuberculate; palp article 1 with several apicodistal setae on medial dorsal margin and numerous marginal setae on ventral margin; article 4 with dense row of oblique and marginal setae on both dorsal and ventral margins; article 3 apical margin and dactyl with dense covering of pubescent setae.

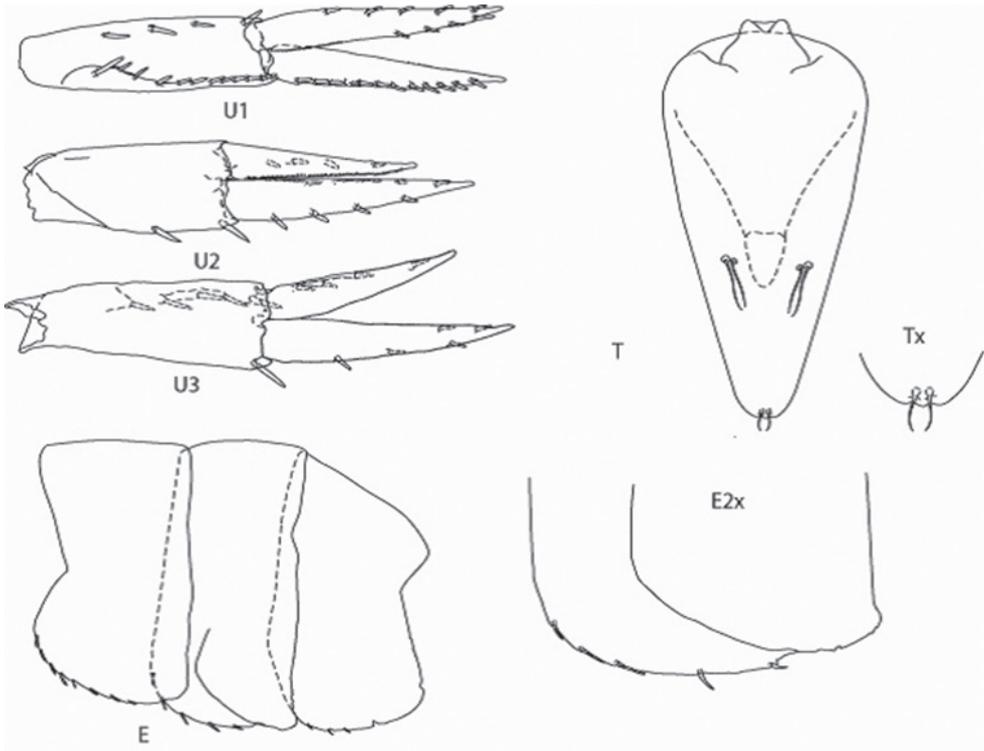


Figure 5. *Leucothoe eltoni* sp. n., holotype ♂A, 8.10 mm; uropods 1-3; epimera, telson.

Gnathopod 1. Coxa lobate, LW 1.25; basis linear, LW 3.66, anterior margin serrate with 22 long setae and single posterodistal apical seta; carpus expanded, basally stout, recurved distally with sharp apex; posterior margin with approximately 49 long recurved setae along 0.18-0.94 of carpal margin and 12 short, submarginal mediofacial setae; propodus, anterior margin greatly inflated, circular, LW 1.50, posterior margin expanded, with approximately 10 short posterior setae; dactyl reduced, straight, closing medially in groove on propodus.

Gnathopod 2. Coxa oval, expanded distally, distal margin smooth, LW 0.87; article 2 linear, LW 4.00, with tuft of six long posterodistal setae; carpal lobe slender, reaching 0.32 along propodus, distal margin expanded and subtruncate, lateral margin serrate, anterior margin oblique, with 15 rows of 6-15 medial setae; propodus, palm oblique, LW 4.25 with three major and two minor projections and two major and two minor concavities, primary mediofacial setal row extending 0.76 of propodus, secondary setal row extending along posterior margin, thicker proximally; dactyl smooth, gently curved, reaching 0.70 of propodus.

Pereopods 3-4. Pereopod 3, coxa elongate ventrally, LW 1.47; basis elongate, antero-distal margin slightly produced, posterior margin with 6 submarginal setae, LW measured at midpoint 6.61; Pereopod 4, coxa distal margin rounded, ventral and posterior margins slightly excavate, posterior margin serrate with 9 small submarginal setae, LW 1.13.



Figure 6. *Leucothoe eltoni* sp. n., male, whole body showing inflated gnathopod1. Photo J. Thomas.

Pereopods 5-7. Coxae of 5-6 bilobed; coxa 7 small, ventrally convex; pereopods 5-7 bases moderately expanded, LW 1.42:1.20:1.09, posterior margin 5-6 smooth, 7 serrate; pereopods 5-7 article four with extended posteroventral lobe reaching 0.92:0.75:0.66 of article 4.

Epimera 1-3. Ventral setae 8:4:3, posterior margins round.

Uropods 1-3. Relative uropod lengths, 1.00: 0.75: 0.77; relative lengths of peduncles 1-3, 1.00:0.84: 0.85; uropod 1, peduncle 1.07 rami length, with 11 medial and 4 lateral setae; outer ramus subequal to inner ramus, with 12 lateral and 0 medial setae, margins minutely crenulate; inner ramus with 4 medial and 5 lateral setae, margins of rami minutely crenulate; uropod 2 peduncle 0.81 rami, with 0 medial and 2 lateral setae; outer ramus 1.30 inner ramus, with 0 medial and 4 lateral marginal setae; outer ramus with 2 medial and 4 lateral marginal setae; margins of rami minutely crenulate; uropod 3, peduncle 0.93 rami, with 1 lateral apical and 5 medial setae; outer ramus 1.34 inner ramus; with 2 medial and 3 lateral marginal setae; outer ramus with 0 medial and 4 lateral marginal setae, margins of rami minutely crenulate.

Telson. LW 1.95, apical margin minutely tridentate, with 2 apical and two pairs of 2 facial setae.

Description of female paratype B, 7.35 mm. Similar to males except for gnathopods 1 and 2. Gnathopod 1, carpus and propodus not greatly inflated, propodus slightly swollen distally. Gnathopod 2, palm of propodus lacking distinct tuberculation and concavities found in males.

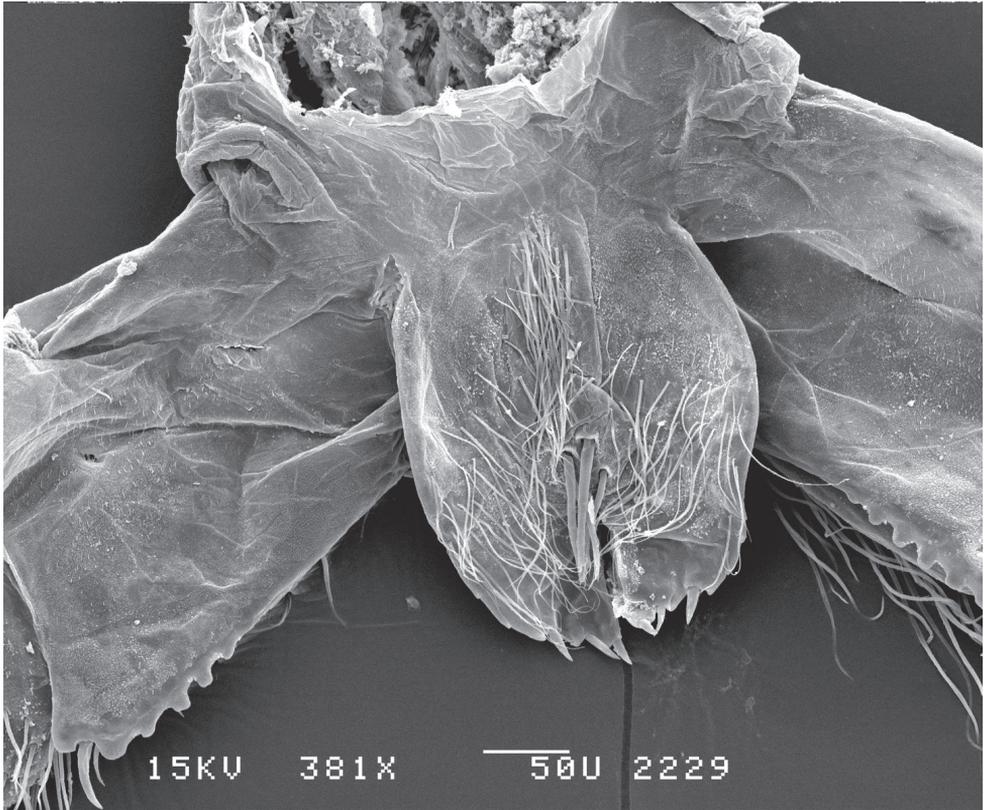


Figure 7. *Leucothoe eltoni* sp. n., SEM, male, maxilliped, 381 \times , Station Indo04-01c, Sulawesi, Indonesia.

Relationships. *Leucothoe eltoni* sp. n. most closely resembles *L. tumida* of Myers (2013) in the inflated carpus and propodus of gnathopod 1; in the short stubby antennae; pereopods 5-7 with article 4 extending more than 50 percent along posterior margin of article 5; and a 2-segmented maxilliped palp. *L. tumida* differs from *L. eltoni* in having a large excavation in the palm of gnathopod 2; and in having a smooth inner margin of the maxilliped outer plate. Both species differ in host preferences with *L. tumida* found in the mantle cavity of the winged pearl oyster *Pteria penguin* while *L. eltoni* prefers branchial chambers of large solitary ascidians, especially *Herdmania* and *Polycarpa* species.

Both *L. tumida* and *L. eltoni* superficially resemble members of the genus *Paraleucothoe* in the large inflated gnathopod 1 of terminal males. However, *Paraleucothoe* differs from all species of *Leucothoe* in having the outer plate of the maxilliped extended distally beyond palp article 1. *Paraleucothoe novaehollandiae* (Haswell, 1879) also has a uniaarticulate maxilla 1 palp but this feature is no longer unique to the genus as a number of recently described *Leucothoe* species have this feature. *Paraleucothoe novaehollandiae* is reported from the branchial chambers of the stalked tunicates *Pyura spinifera*

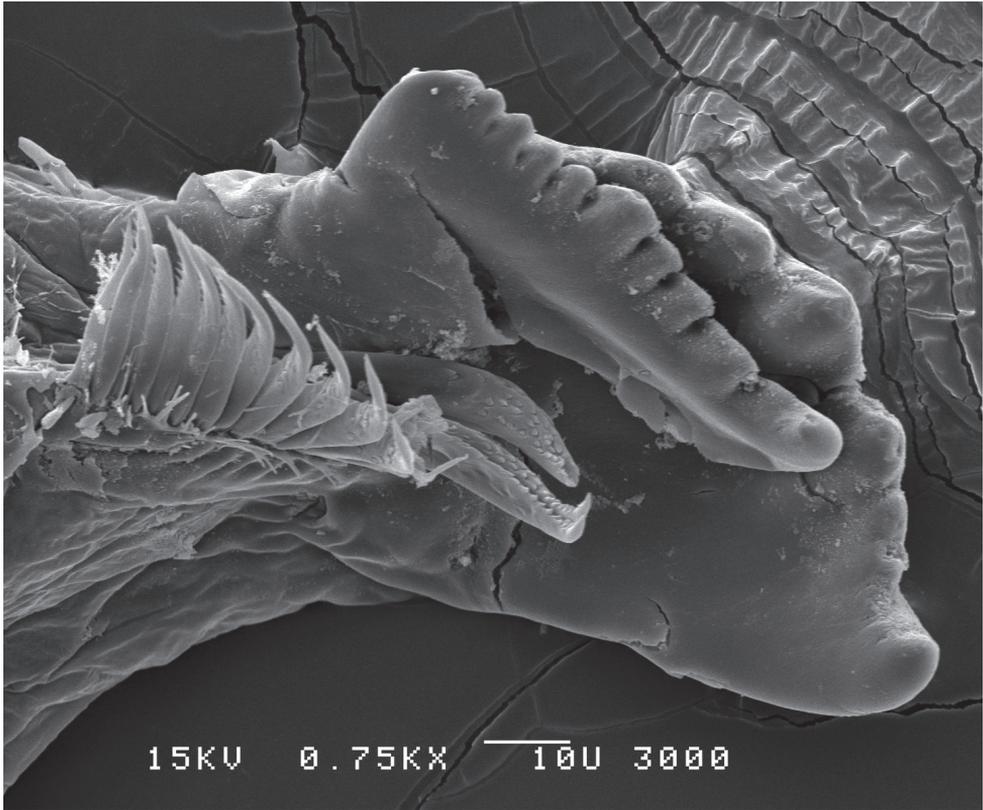


Figure 8. *Leucothoe eltoni* sp. n., SEM, male, left mandible, 400 \times ; Station Indo04-01c, Sulawesi, Indonesia.

and *P. praeputialis* (formerly *P. stolonifera*) in southern Australia waters (Lowry et al 2000) and other large solitary tunicates such as *Herdmania* sp. The exact placement of *Paraleucothoe flindersi* described by Stebbing (1888) from the Torres Straits remains problematic as it lacks the extended apical lobe of maxilliped outer plate typical of *L. novaehollandiae*, but has a uniarticulate palp and gnathopod 1 reminiscent of *L. eltoni* females and juvenile males. Further resolution awaits examination of material from the type locality.

Ecology. Coral reefs, coral rubble, found primarily in branchial baskets of solitary tunicates such as *Herdmania* and *Polycarpa* sp., rarely in bivalve mollusks (winged pearl oyster *Pteria penguin*), and branched yellow rope sponges *Callyspongia* (species undetermined).

Distribution. Indonesia: Celebes Sea, Sulawesi, Kri Island, Halmera Sea, Raja Ampat Islands. Philippines: Cape Verde Passage, Mabini Tingloy. Hawaiian Islands (invasive): Ohau to Molokai, 2–20m.

Discussion. While the native range of *L. eltoni* sp. n. encompasses shallow coral reef habitats in Indonesian and the Philippines, it is also an established invasive in

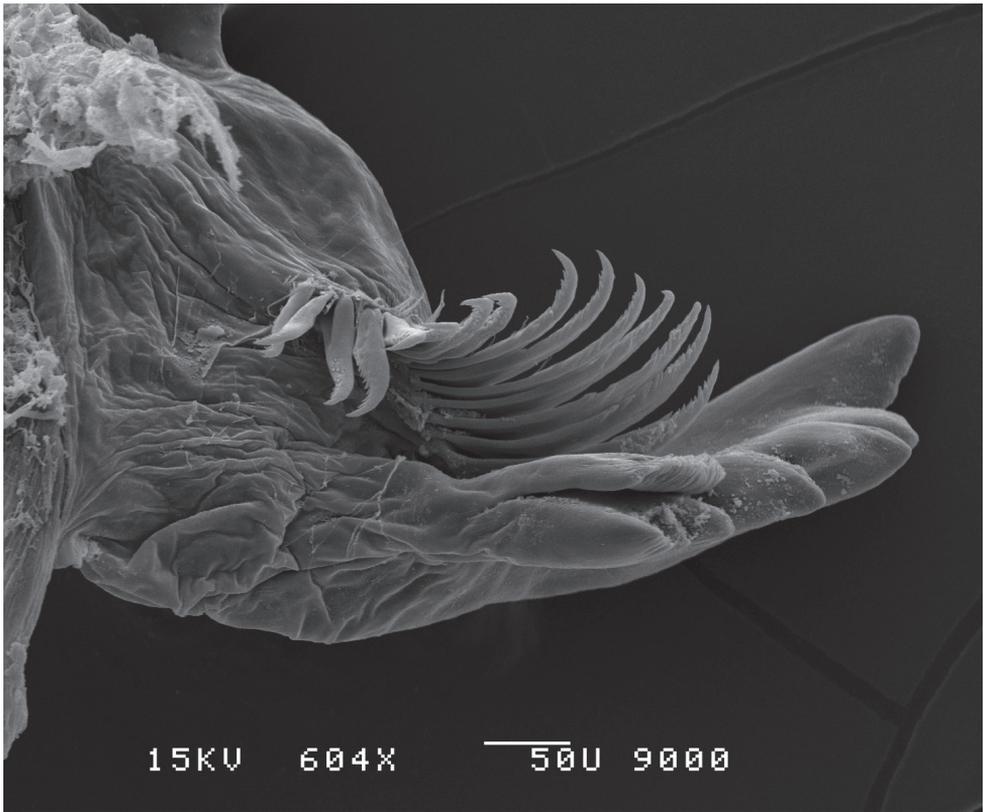


Figure 9. *Leucothoe eltoni* sp. n., SEM, male, right mandible, 600 \times ; Station Indo04-01c, Sulawesi, Indonesia.

Hawaiian waters (Coles et al. 1999). The most likely vector for introduction was a dry dock, USS *Machinist*, transported to Pearl Harbor from Subic Bay, Philippines in 1992. Prior extensive treatment of Hawaiian amphipods by J.L. Barnard (1970, 1971) and ongoing monitoring by the Bishop Museum did not document any leucothoid resembling *L. eltoni* sp. n. prior to 1992. Ongoing sampling of marine flora and fauna by the Bishop Museum first reported this species in 1997 as *Paraleucothoe flindersi*. Muir (1997) speculated it was most likely an introduced species. Such rafting on floating metal objects is a possible means of transportation for benthic marine organism (Cairns 2000; Creed and de Paula 2007, Hoeksema et al. 2012). Since first reported from Pearl Harbor in 1997 (as *Paraleucothoe flindersi*) *L. eltoni* sp. n. has spread throughout Oahu and other islands including Molokai. The author has collected *L. eltoni* sp. n. from sponges in Kaneohe Bay, Ohau. The effects, if any, of this species on endemic leucothoid commensals and its spread in Hawaii is unknown at this time.

Acknowledgements

The author wishes to thank Dr. Bert W. Hoeksema (Naturalis Biodiversity Center) and Mrs. Yosephine Tuti (RCO-LIPI) who jointly organized the Raja Ampat (2007) expedition. The Indonesian Institute of Sciences (LIPI) granted the research permit. The research was accommodated by Papua Diving at Kri Island, Raja Ampat. Additional funding was provided to the author by a Temminck Fellowship from Naturalis Biodiversity Center, Leiden, the Netherlands, and by the Reef Foundation, Inc., USA. The author also wishes to thank Ken Longenecker and Steve Coles of the Bishop Museum, Hawaii, for first calling his attention to the presence of this species in Hawaiian waters and making museum collections available for study.

The author also thanks Terry Gosliner from the California Academy of Sciences for field support in the Philippines. Additionally, the author wishes to recognize the Philippines Department of Agriculture Bureau of Fisheries and Aquatic Resources (DA-BFAR), and the Philippines National Fisheries Research and Development Institute (NFDRI) for their regulatory and administrative support for the Verde Island Passage (VIP) project. This research was also supported by a grant from National Science Foundation DEB 12576304 PEET grant to Terrence Gosliner, Richard Mooi, Luis Rocha and Gary Williams to inventory the biodiversity of the Verde Island Passage.

References

- Barnard JL (1970) Sublittoral gammaridea (Amphipoda) of The Hawaiian Islands. *Smithsonian Contributions to Zoology* 34: 286, figs 180.
- Barnard JL (1971) Keys to the Hawaiian marine gammaridea, 0-30 meters. *Smithsonian Contributions to Zoology* 58: 135, figs 68.
- Barnard JL (1972) Gammaridean Amphipoda of Australia, Part I. *Smithsonian Contributions to Zoology* 103: 333, figures 1–194. doi: 10.5479/si.00810282.103
- Cairns SD (2000) A revision of the shallow-water azooxanthellate Scleractinia of the Western Atlantic. *Studies of the Natural History of the Caribbean Region* 75: 1–240.
- Carlton, James T (2010) The impact of maritime commerce on marine biodiversity. *The Brown Journal of World Affairs* 16: 131–142.
- Coles SL, DeFelice RCE, Eldredge LG, Carlton JT (1999) Historical and recent introductions from non-indigenous marine species into Pearl Harbor, Oahu, Hawaiian, Islands. *Marine Biology* 135: 147–158. doi: 10.1007/s002270050612
- Creed JC, de Paula AF (2007) Substratum preference during recruitment of two invasive alien corals onto shallow subtidal tropical rocky shores. *Marine Ecology Progress Series* 330: 101–111. doi: 10.3354/meps330101
- Felgenhauer BE (1987) Techniques for preparing crustaceans for scanning electron microscopy. *Journal of Crustacean Biology* 7: 71–76. doi: 10.2307/1548626
- Hoeksema BW (2007) Delineation of the Indo-Malayan Centre of Maximum Marine Biodiversity: The Coral Triangle. In: Renema R (Ed.) *Biogeography, Time and Place: Distri-*

- butions, Barriers and Islands, Springer, Dordrecht, 117–178. doi: 10.1007/978-1-4020-6374-9_5
- Hoeksema BW, van der Meij SET (2008) <http://www.repository.naturalis.nl/document/124392>
- Hoeksema BW, Roos PJ, Cadée GC (2012) Trans-Atlantic rafting by the brooding reef coral *Favia fragum* on man-made flotsam. *Marine Ecology Progress Series* 445: 209–218. doi: 10.3354/meps09460
- Krapp-Schickel T, De Broyer C (2014) Revision of *Leucothoe* (Amphipoda, Crustacea) from the Southern Ocean: a cosmopolitanism concept is vanishing. *European Journal of Taxonomy* 80: 1–55. doi: 10.5852/ejt.2014.80
- Lowry JK, Berents PB, Springthorpe RT (2000) Australian Amphipoda: Leucothoidae. Version 1: 2 October 2000. <http://www.crustacea.net/>
- Muir DG (1997) New records of Peracarid crustacea in Hawaii (Crustacea: Peracarida). Records of the Hawaiian Biological Survey for 1996—Part 2: Notes. In: Evenhuis NL, Miller SC (Eds) Bishop Museum Occasional Papers 49: 50–54.
- Myers AA (2013) Amphipoda (Crustacea) from Palau, Micronesia: Families Dexaminidae, Eusiridae, Hyalidae, Ischyroceridae, Leucothoidae and Lysianassidae. *Zootaxa* 3731(3): 301–323. doi: 10.11646/zootaxa.3731.3.1
- Ortiz M, Winfield I (2012) A New Commensal Species of the Genus *Leucothoe* Leach, 1814 (Amphipoda: Leucothoidae) from the Cuban Archipelago. *Travaux du Muséum National d’Histoire Naturelle “Grigore Antipa”* 55(1): 17–26.
- Reish DR, Barnard JL (1979) Amphipods (Arthropoda:Crustacea:Amphipoda). In: Hart CW, Fuller SLH (Eds) Pollution ecology of estuarine invertebrates. Academic Press, New York, 1–406.
- Thomas JD (1979) Occurrence of the amphipod *Leucothoides pottsi* Shoemaker in the tunicate *Ecteinascidia turbinata* Herdman from Big Pine Key, Florida. *Crustaceana* 37(1): 107–109. doi: 10.1163/156854079x00104
- Thomas JD (1993) Biological monitoring and tropical biodiversity in marine environments: A critique with recommendations, and comments on the use of amphipods as bioindicators. *Natural History* 27: 795–806. doi: 10.1080/00222939300770481
- Thomas JD (1997a) Systematics and Phylogeny of the commensal amphipod family Anamixidae (Crustacea: Amphipoda). *Records of the Australian Museum* 49: 3–98, figures 1-27-187.
- Thomas JD (1997b) Using Marine Invertebrates to Establish Research and Conservation Priorities. In: Reaka-Kudla ML, Wilson DE, Wilson EO (Eds) Biodiversity II: Understanding and protecting our biological resources. Joseph Henry Press, Washington, D.C., 357–370.
- Thomas JD, Klebba KN (2006) Studies of commensal leucothoid amphipods: two new sponge-inhabiting species from south Florida and the western Caribbean. *Journal of Crustacean Biology* 26(1): 13–22. doi: 10.1651/C-2624.1
- Thomas JD, Barnard JL (1983) Transformation of the *Leucothoides* morph to the *Anamixis* morph (Amphipoda). *Journal of Crustacean Biology* 3(1): 154–157. doi: 10.2307/1547860
- Thomas JD, Klebba KN (2007) New species and host associations of commensal leucothoid amphipods from coral reefs in Florida and Belize (Crustacea: Amphipoda). *Zootaxa* 1494: 1–44.

- Thomas JD, Krapp-Schickel T (2011) A new species of Leucothoid Amphipod, *Anamixis bananarama*, sp. n., from Shallow Coral Reefs in French Polynesia (Crustacea, Amphipoda, Leucothoidae). *ZooKeys* 92: 1–8. doi: 10.3897/zookeys.92.1036
- Thomas JD, White KN (2014) Leucothoidae database, Current Leucothoidae species (version 3.14), <http://www.nova.edu/ocean/jthomas/apod.html>
- White KN (2011a) Nuclear 18S rDNA as a species-level molecular marker for the Leucothoidae (Amphipoda). *Journal of Crustacean Biology* 31(4): 710–716. doi: 10.1651/11-3489.1
- White KN (2011b) A Taxonomic review of the Leucothoidae (Crustacea: Amphipoda). *Zootaxa* 3078: 1–113.
- White KN (2012) Seasonal patterns in leucothoid amphipods (Crustacea: Amphipoda: Leucothoidae). *Marine Biodiversity* 42(4): 453–457. doi: 10.1007/s12526-012-0123-6
- White KN (2013a) Connecting the dots: confirmation and description of *Paranamixis misakiensis* Thomas, 1997 leucomorphs (Amphipoda: Leucothoidae). *Crustaceana* 86(4): 403–415. doi: 10.1163/15685403-00003186
- White KN (2013b) All things in moderation: Using formalin to coerce leucothoid amphipods out of the rubble (Crustacea: Amphipoda: Leucothoidae). *Marine Biodiversity* 43(2): 163–166. doi: 10.1007/s12526-012-0126-3
- White KN, Reimer JD (2012a) Commensal Leucothoidae (Crustacea, Amphipoda) of the Ryukyus Archipelago, Japan. Part I: ascidian-dwellers. *ZooKeys* 163: 13–55. doi: 10.3897/zookeys.163.2003
- White KN, Reimer JD (2012b) Commensal Leucothoidae (Crustacea, Amphipoda) of the Ryukyus Archipelago, Japan. Part II: sponge-dwellers. *ZooKeys* 166: 1–58. doi: 10.3897/zookeys.166.2313
- White KN, Reimer JD (2012c) Commensal Leucothoidae (Crustacea, Amphipoda) of the Ryukyus Archipelago, Japan. Part III: coral rubble-dwellers. *ZooKeys* 173: 11–50. doi: 10.3897/zookeys.173.2498
- White KN, Reimer JD (2012d) DNA phylogeny of Leucothoidae (Crustacea: Amphipoda) from the Ryukyu Archipelago, Japan. *Contributions to Zoology* 81(3): 159–165.
- White KN, Thomas JD (2009) Leucothoidae. In: Lowry JK, Myers AA (Eds) Amphipoda (Crustacea: Peracarida) of the Great Barrier Reef, Australia. *Zootaxa* 2260: 494–555.
- Winfield I, Alvarez F (2009) Two New Species of Amphipods (Peracarida, Amphipoda, Leucothoidae) from the Veracruz Coral Reef System, S.W. Gulf of Mexico. *Crustaceana* 82(1): 11–25. doi: 10.1163/156854008x367214
- Winfield I, Ortiz M, Cházraro-Olivera S (2009) A new species of commensal amphipod (Amphipoda: Gammaridea: Leucothoidae) from Veracruz coral reef system, SW Gulf of Mexico. *Revisita Mexicana de Biodiversidad* 80: 315–320.

Does the genetic structure of spring snail *Bythinella* (Caenogastropoda, Truncatelloidea) in Bulgaria reflect geological history?

Artur Osikowski¹, Dilian Georgiev², Sebastian Hofman¹, Andrzej Falniowski³

1 Department of Comparative Anatomy, Institute of Zoology, Jagiellonian University, Gronostajowa 9, 30–387, Kraków, Poland **2** Department of Ecology and Environmental Conservation, University of Plovdiv, Tzar Assen Str. 24, BG-4000 Plovdiv, Bulgaria **3** Department of Malacology, Institute of Zoology, Jagiellonian University, Gronostajowa 9, 30–387, Poland

Corresponding author: Sebastian Hofman (s.hofman@uj.edu.pl)

Academic editor: Frank Köhler | Received 23 May 2015 | Accepted 13 August 2015 | Published 25 August 2015

<http://zoobank.org/837828DA-FB6F-43FF-959B-A95CD8512E61>

Citation: Osikowski A, Georgiev D, Hofman S, Falniowski A (2015) Does the genetic structure of spring snail *Bythinella* (Caenogastropoda, Truncatelloidea) in Bulgaria reflect geological history? ZooKeys 518: 67–86. doi: 10.3897/zookeys.518.10035

Abstract

Bythinella is a minute dioecious caenogastropod that inhabits springs in central and southern Europe. In the Balkans, previous studies have addressed its morphological and genetic differentiation within Greece and Romania while the Bulgarian species have remained poorly known. The aim of the present paper has been to expand the knowledge on the subject in Bulgaria. Shell morphology and anatomy of the reproductive organs were examined, and a fragment of the mitochondrial cytochrome oxidase subunit I (COI) gene and the nuclear ribosomal Internal Transcribed Spacer 1 (ITS-1) were sequenced from 15 populations. Additional sequences from eight previously studied populations were included in our analyses. Phylogenetic analyses revealed five main mitochondrial DNA clades, which were partly confirmed by analyses of the ITS-1 sequences. The genetic differentiation between the clades was found to be in the range $p=2.4$ –11.8%. Most of the populations belonged to clade I, representing *B. hansboetersi*, and were distributed in SW Bulgaria. Clades II and III inhabit areas adjacent to clade I and were most closely related with the latter clade. Much more distinct were clade V, found at one locality in NW Bulgaria, and clade IV, found at one locality in SE Bulgaria, close to the sea. Four populations were found in caves, but only one of these represented a distinct clade. Considering the observed pattern of interpopulation differentiation of *Bythinella* in Bulgaria, we can suppose that isolation between clades I, II and III may have been caused

by glaciations during the Pleistocene. The time of isolation between the above three clades and clade IV coincides with the Messinian Salinity Crisis, and the time of isolation between the clade V and the other four most probably reflects the isolation of the Rhodopes from western Balkan Mts by the seawater of the Dacic Basin.

Keywords

Gastropoda, phylogeography, Balkans, Messinian Salinity Crisis, Dacic Basin

Introduction

The genus *Bythinella* Moquin-Tandon, 1856 consists of minute (2–4 mm shell height), dioecious, oviparous freshwater snails inhabiting springs and subterranean waters across Europe and western Asia. In Europe, their range extends from the Iberian Peninsula to the Ukraine, and from southern Poland and Germany, to Sicily and Crete. These snails also occur on numerous Mediterranean islands and in the western part of Turkey (Falniowski et al. 2012; Benke et al. 2011).

Early studies on *Bythinella* taxonomy mainly concentrated on the morphology of the shell and, later, the external morphology and anatomy of the body (e.g., Boeters 1973, 1998; Radoman 1976; Falniowski 1987). It has been demonstrated, however, that morphology alone cannot be used for unequivocal species delimitation due to the limited number of taxonomically useful characters and their large variability (Falniowski 1987, 1992; Falniowski et al. 2009a; Bichain et al. 2007a, b). Recent molecular studies (Bichain et al. 2007a; Haase et al. 2007; Benke et al. 2011; Falniowski et al. 2009a, b, 2012; Falniowski and Szarowska 2011, 2012) have led to revised species delimitations. For *Bythinella* an allopatric mode of speciation and distribution of the species has generally been postulated. This caused authors to overestimate the importance and effectiveness of geographical isolation. This partly triggered numerous descriptions of new species, which were based solely on the occurrence of snails in springs not previously studied. However, the real amounts of gene flow between local populations of *Bythinella* is high (Falniowski et al. 1998, 1999, Falniowski and Szarowska 2011), and there have been even sympatric occurrences of two species of *Bythinella* in the same spring (Radoman 1976, Falniowski et al. 2009b, Falniowski and Szarowska 2011).

In Bulgaria, several *Bythinella* species have been described solely on the basis of morphological characters, including only shell and penis: *B. ravnogorica*, Glöer and Georgiev 2009, *B. rhodopensis*, Glöer and Georgiev 2009, *B. srednogorica*, Glöer and Georgiev 2009, *B. markovi*, Glöer and Georgiev 2009, *B. walkeri*, Glöer and Georgiev 2009, (Glöer and Georgiev 2009), *B. rilaensis*, Glöer and Georgiev 2011, *B. slaveyae*, Glöer and Georgiev 2011, *B. angelovi*, Glöer and Georgiev 2011 (Glöer and Georgiev 2011), *B. cf. opaca*, von Gallenstein 1848 (Georgiev and Stoycheva 2008; later described as *B. srednogorica*), *B. gloeri*, Georgiev 2009 (Georgiev 2009), *B. hansboetersi*, Glöer and Pešić 2006 (Glöer and Pešić 2006) and *B. stoychevae*, Georgiev 2011 (Georgiev

2011). In *Bythinella*, the shell as well as the penis exhibit substantial variability, often even within populations (Falniowski 1987), including all the character states considered by the authors cited above. Last but not least, the species-level taxonomy of *Bythinella* is heavily flawed by common assumption that different localities should harbour different species. Molecular studies by Falniowski et al. (2009a) on five populations from Bulgaria revealed low inter-population genetic distances, leading to the conclusion that all of them belonged to the same species. This result strongly suggests that it is necessary to incorporate the study of molecular markers in critical revisions of the *Bythinella* species in Bulgaria.

The palaeogeographic history of central and southern Europe has significantly influenced the distribution of fauna and flora in this region. An ecological event with a large impact on biodiversity in present day Bulgaria and Romania was the flooding of the Dacic Basin with seawater. This basin separated the Carpathians from central Bulgaria (Suc et al. 2011) from about 8 until about 1.8 Million years ago (Mya). Previous research has indicated that the genetic divergence of *Bythinella* is much higher in neighbouring Romania than in Bulgaria, suggesting that the Dacic Basin may have caused the extinction of this genus in a vast parts of Bulgaria (Falniowski et al. 2009b, 2012). However, this scenario was suggested based on limited sampling in Bulgaria and, therefore, requires further study.

Among many nominal species of *Bythinella* described in Bulgaria on the basis of morphological characters, some cave taxa have been identified. *B. markovi* was reported from the Gargina Dupka Cave (Glöer and Georgiev 2009, 2011; Georgiev and Glöer 2013) and *B. gloeeri* from Lepenitsa Cave in the Rhodopes (Georgiev 2009). These two caves are situated about 80 km apart from each other as the crow flies in different ridges of the Rhodopes as parts of different river catchments. These two species differ substantially in their morphology. Current phylogeographic studies confirmed theoretical assumptions that cave animal taxa are often cryptic and possess highly restricted geographical distributions despite potential gene flow from surface populations (Juan et al. 2010). To test this hypothesis on Bulgarian *Bythinella*, confirmation of its distinctness, previously described on basis of morphological characters, is necessary using molecular techniques. Since low genetic differentiation between the surface *Bythinella* population in Bulgaria has been reported (Falniowski et al. 2009a), more data on the phylogenetic differentiation of potentially distinct cave species is needed.

The aim of our study has been to improve the knowledge of *Bythinella* distribution in Bulgaria through extended sampling and to answer the following questions: 1) Is the low genetic divergence previously reported for Bulgarian *Bythinella* a fact or the result of poor sampling? 2) Are the biogeographical patterns and phylogenetic relationships of *Bythinella* correlated with the geological history of the region? 3) Have the cave populations of *Bythinella* been isolated for a long time from the ones in surface water reservoirs? 4) Do molecular data support the opinion of Glöer and Georgiev (2011) about Bulgaria as a hot-spot of diversity of *Bythinella*? To answer these questions, both morphological (shell) and molecular (COI and ITS-1 genetic markers) characters were examined.

Materials and methods

Snail sampling and fixation

Bythinella snails were collected from 15 sites across Bulgaria (Fig. 1, Table 1). In four of these sites the snails were found in caves. Six of the studied populations were from the type localities of the nominal species.

Snails were collected by hand or with a sieve. Individuals for the morphological study were fixed in 4% formaldehyde and stored in 80% ethanol, while individuals for molecular analyses were washed in 80% ethanol and left to stand in it for about 12 hours. The ethanol was then changed twice during 24 hours and, after a few days, samples were transferred to 96% ethanol and stored at -20 °C prior to DNA extraction.

DNA extraction and sequencing

DNA was extracted from foot tissue using the SHERLOCK extracting kit (A&A Biotechnology) and dissolved in 20 µl TE buffer. PCR was performed in the reaction mixture of 50 µl total volume using the following primers: LCOI490 (Folmer et al. 1994) and COR722b (Wilke and Davis 2000) for the COI gene, and two *Bythinella*-specific primers ITS1D and ITS1R for the ITS-1 (Bichain et al. 2007). The PCR conditions were as follows. COI – initial denaturation step of 4 min at 94 °C, followed by 35 cycles at 94 °C for 1 min, 55 °C for 1 min, 72 °C for 2 min, and a final extension of 4 min at 72 °C; ITS-1 – initial denaturation step of 4 min at 94 °C, followed by 25 cycles at 94 °C for 30 s, 60 °C for 30 s, 72 °C for 30 s, and a final extension of 5 min at 72 °C. Ten µl of the PCR product was run on 1% agarose gel to check for quality. PCR products were purified using Clean-Up columns (A&A Biotechnology). The purified PCR products were sequenced in both directions using BigDye Terminator v3.1 (Applied Biosystems) following the manufacturer's protocol and using the primers described above. The sequencing reaction products were purified using ExTerminator Columns (A&A Biotechnology), and the sequences were read using an ABI Prism sequencer.

Morphological studies

Snails were dissected under a NIKON SMZ-U stereo-microscope with a NIKON drawing apparatus, and a CANON EOS 50D digital camera was used to photograph the shells.

Data analysis

Sequences were edited in Bioedit 7.1.3.0 (Hall 1999) and aligned with the ClustalW program in MEGA 6 (Tamura et al. 2013). Single ITS sequences were assembled and

Table 1. The sampling localities with their geographical coordinates, and the haplotypes for COI and ITS genes detected in each locality. Sequences from GenBank are also included. Compare with Figure 1.

ID	Taxon	Site	Coordinates	COI haplotypes	ITS haplotypes
B1	<i>B. sp.</i>	Bulgaria - Bezbog Peak, Pirin Mts.	41°45'20"N; 23°32'39"E	HB1×3	HB1×3
B2	<i>B. sp.</i>	Bulgaria - Ribarits village, Stara Planina Mts.	42°49'33"N; 24°22'23"E	HB2A×3, HB2B	HB2A, HB2B
B3	<i>B. sp.</i>	Bulgaria - Leshnitski Waterfall, Belasitsa Mts.	41°22'12"N; 23°11'12"E	HB3A, HB3B×3	HB3
B4	<i>B. sp.</i>	Bulgaria - Panagyurski Kolonii, Sredna Gora Mts.	42°34'20"N; 24°12'34"E	HB2A×3	HB2B×2
B5	<i>B. sp.</i>	Bulgaria - Nestinarka beach, Strandzha Mts.	42°09'16"N; 27°51'21"E	HB5×6	-
B6	<i>B. sp.</i>	Bulgaria - N of Pnitsite area, Stara Planina Mts.	42°39'44"N; 24°58'40"E	HB6×5	HB2A×2
B7	<i>B. gloeeri</i>	Bulgaria - Lepenitza cave, West Rhodopes Mts.	41°57'14"N; 24°00'43"E	HB7A, HB7B×5	HB7×5
B8	<i>B. stoychevae</i>	Bulgaria - Manuilova Dupka Cave, Rhodopes Mts.	41°42'53"N; 23°46'58"E	HB8×5	HB8×2
B9	<i>B. namogorica</i>	Bulgaria - Ravnogor village, West Rhodopes Mts.	41°57'00"N; 24°21'53"E	HB9A, HB9B×2	-
B10	<i>B. sp.</i>	Bulgaria - Vodni Pech Cave	43°30'11"N; 22°46'55"E	HB10A×2, HB10B, HB10C×3	HB10A×2, HB10B, HB10C×2
B11	<i>B. angelovi</i>	Bulgaria - Koprivskitsa town, Sredna Gora Mts.	42°08'14"N; 24°21'55"E	HB11	HB2A
B12	<i>B. rhodopensis</i>	Bulgaria - Modarskata Cave, West Rhodopes Mts.	41°52'40"N; 24°33'40"E	HB12×3	HB2A×2
B13	<i>B. rildensis</i>	Bulgaria - Rila Mts., near Belovo	42°08'15"N; 23°58'00"E	HB7B×2	HB7×4
B14	<i>B. dierkingi</i>	Bulgaria - Ravnogor village, West Rhodopes Mts.	41°56'59"N; 24°22'02"E	HB11×3	HB2A×4
B15	<i>B. sp.</i>	Bulgaria - Koprivshitsa town, Sredna Gora Mts.	42°38'15"N; 24°21'57"E	HB11×4	HB2A×2, HB2B
Falniowski et al. 2009b (FJ545011–FJ545131)					
1	<i>B. viscutiana</i>	Romania - Vișeu River Valley	47°52'14"N; 24°11'23"E	HR1A×3, HR1B×6	HR1×2
2	<i>B. molcsanyi</i>	Romania - Igniș Mts., western slope of Firiza Lake	47°43'02"N; 23°36'29"E	HR2A×2, HR2B×5	HR2A, HR2B
3	<i>B. molcsanyi</i>	Romania - Igniș Mts., upstream of locality 2	47°45'58"N; 23°38'32"E	HR2A×3, HR3A×5, HR3B×2	HR2B×2
4	<i>B. molcsanyi</i>	Romania - Igniș Mts., near Izvoare Resort	47°45'14"N; 23°42'28"E	HR3A×2, HR4A×4, HR4B×3	HR4A×2, HR4B
5	<i>B. molcsanyi</i>	Romania - Igniș Mts., Izvoare Resort	47°44'51"N; 23°43'03"E	HR2B×12, HR4B×8	HR5A, HR5B, HR5C, HR5D
6	<i>B. radomani</i>	Romania - Bihor Mts., close to Vărtop Pass	46°31'25"N; 22°37'25"E	HR6A×5, HR6B×3	HR6A×2, HR6B, HR6C, HR6D
7	<i>B. radomani</i>	Romania - Bihor Mts., Iarba Rea village	46°25'35"N; 22°46'29"E	HR7×7	HR7×3
8	<i>B. dacica</i>	Romania - Retezat Mts., La Beci, Buta river valley	45°18'26"N; 22°56'12"E	HR8A×6, HR8B×4, HR8C×3	HR8A, HR8B
9	<i>B. dacica</i>	Romania - Retezat Mts., Râu Șes valley	45°19'25"N; 22°40'51"E	HR9A×3, HR9B×4	HR9A, HR9B×2, HR9C

ID	Taxon	Site	Coordinates	COI haplotypes	ITS haplotypes
10	<i>B. dacica</i>	Romania - Cerna Valley	45°00'33"N; 22°32'40"E	HR10A×2, HR10B×4	HR10A, HR10B, HR10C
11	<i>B. dacica</i>	Romania - Cerna Valley, 3.5 km up from locality 10	45°02'10"N; 22°34'06"E	HR10A×6, HR11×6	HR10B×2
12	<i>B. calimaniica</i>	Romania - Călimani Mts.	46°57'10"N; 25°04'07"E	HR12A×3, HR12B×4, HR12C×6	-
Falniowski et al. 2009a (GQ152518–GQ152544)					
13	<i>B. hansboetersi</i>	Bulgaria - Smoljan town, below Smoljanske Lake	41°37'01"N; 24°40'31"E	HBUI13A×2, HBUI13B×2, HBUI13C	HB2A, H13A, HBUI13B
14	<i>B. hansboetersi</i>	Bulgaria - Smoljan town, near Amzovo	41°33'42"N; 24°41'41"E	HB2A×2, HBUI14A×3, HBUI14B×2	HBUI13B, HBUI14
15	<i>B. hansboetersi</i>	Bulgaria - Anton town, Bolovan Hill	42°44'48"N; 24°16'51"E	HB2A×3, HBUI15A×3, HBUI15B, HBUI15C	HB2B×5, HBUI15
16	<i>B. hansboetersi</i>	Bulgaria - Mugla village	41°37'43"N; 24°31'08"E	HBUI16A×4, HBUI16B×3	HBUI16A×2, HBUI16B
Falniowski et al 2012. (JQ639859–JQ639883)					
17	<i>B. hansboetersi</i>	Bulgaria - Stara Planina, spring of Cherni Osam	42°43'21"N; 24°46'47"E	HBUI15B	-
18	<i>B. srednogorica</i>	Bulgaria - Sredna Gora Mts., S. of Streltcha town	42°27'16"N; 24°20'27"E	HB2A×2, HBUI18	-
19	<i>B. rhodopensis</i>	Bulgaria - West Rhodopes Mts., S. of Lilkovo village	41°52'39"N; 24°33'21"E	HBUI19A, HBUI19B, HBUI19C	-
20	<i>B. slavayae</i>	Bulgaria - Belasits Mts., S. of Belasitsa village	41°21'07"N; 23°09'19"E	HB2A×2, HBUI20	-
21	<i>B. nonveilleri</i>	Serbia - Rtanj Mt., Vrmd a spring	43°42'00"N; 21°49'00"E	HSE21A×2, HSE21B	-
22	<i>B. pesterica</i>	Serbia - Pester Plateau, Djerekare village	43°00'00"N; 20°08'00"E	HSE22A, HSE22B, HSE22C	-
23	<i>B. taranensis</i>	Montenegro - canyon of the river Tara, stream Ljevok	42°59'29"N; 19°25'53"E	HMO23A×2, HMO23B	-
24	<i>B. luteola</i>	Montenegro - National Park Biogradska Gora	42°53'31"N; 19°36'16"E	HMO24	-
25	<i>B. dispersa</i>	Montenegro - spring in Petnjik village	42°49'35"N; 19°54'10"E	HMO25A, HMO25B, HMO25C	-

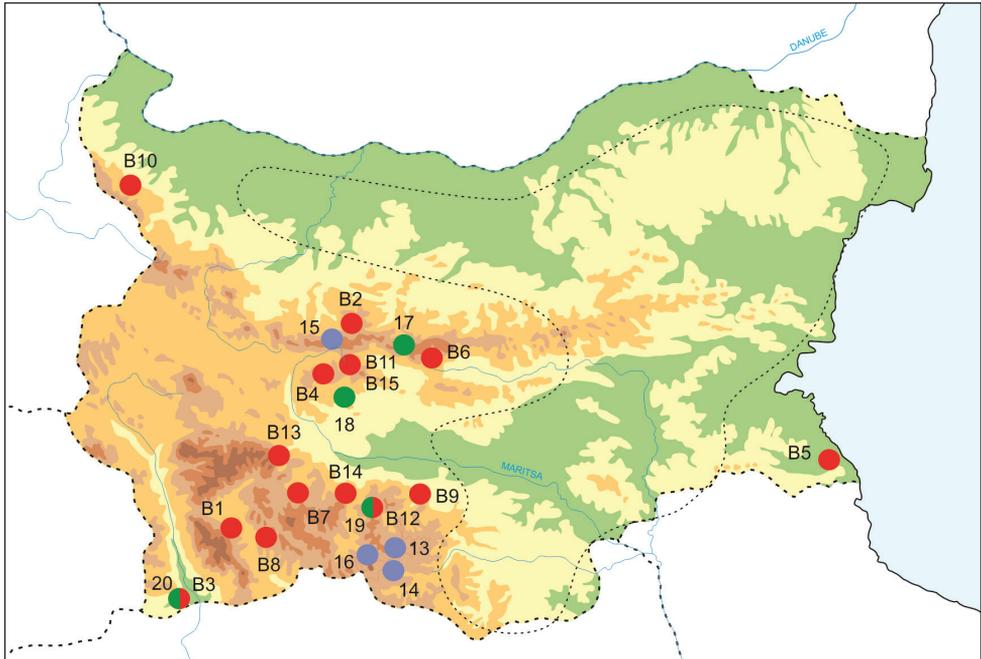


Figure 1. Sampling sites used in the present study (red dots) and in phylogenetic analyses (blue dots: Falniowski et al. 2009a; green dots: Falniowski et al 2012). Compare with Table 1. The dotted line indicates an area that was searched but where no *Bythinella* sites were found.

aligned using CodonCodeAligner 4.2.7 (CodonCodeCorporation, Dedham, MA). Basic sequence statistics, including haplotype polymorphism and nucleotide divergence, were calculated in DnaSP 5.10 (Librado and Rozas 2009). The saturation test of Xia et al. (2003) was performed using DAMBE (Xia 2013).

Sequences obtained from *Bythinella* specimens in the present work were used in a phylogenetic analysis with other sequences obtained from GenBank (Table 1). The data were analysed using Bayesian inference (BI) and the maximum likelihood (ML) approach. We applied the GTR + I + Γ model because over-parameterization seems to be less dangerous for BI analyses than under-parameterization (Huelsenbeck and Ronquist 2004). For ML analyses, GTR + I + Γ is the only nucleotide substitution model implemented in RAxML.

The Bayesian analyses were run with MrBayes ver. 3.2.3 (Ronquist et al. 2012) using default priors. Two simultaneous analyses were performed, each lasting 10,000,000 generations, with one cold chain and three heated chains, starting from random trees and sampling trees every 1000 generations. The first 25% trees were discarded as burn-in. The analyses were summarised on a 50% majority-rule tree.

A maximum likelihood (ML) approach was conducted in RAxML v8.0.24 (Stamatakis 2014). One thousand searches were initiated with starting trees obtained through the randomized stepwise addition maximum parsimony method. The tree with the highest likelihood score was considered as the best representation of the phylogeny.

Bootstrap support was calculated with 1000 replicates and summarized onto the best ML tree. RAxML analyses were performed using free computational resource CIPRES Science Gateway (Miller et al. 2010).

To infer haplotype networks of the markers used, a median-joining calculation was implemented in NETWORK 4.6.1.1 (Bandelt et al. 1999).

To test the molecular clock, COI data were used. Two hydrobiids, *Peringiaulvae* Pennant, 1777 and *Salenthydrobia ferreri* Wilke, 2003 (AF478401, AF478410) were used as outgroups. The divergence time between these two species (5.96 Mya) was used to calibrate the molecular clock, with correction according to Falniowski et al. (2008), since the isolation started with the beginning, not the end of the Messinian Salinity Crisis. The likelihoods for trees with and without the molecular clock assumption for a Likelihood Ratio Test (LRT) (Nei and Kumar 2000) were calculated with PAUP. The Relative Rate Test (RRT) (Tajima 1993) was performed in MEGA. As Tajima's RRTs and the LRT test rejected the equal evolutionary rate throughout the tree for *Pseudamnicola*, time estimates were calculated using a non-parametric rate smoothing (NPRS) analysis with the recommended Powell algorithm, in r8s v.1.7 for Linux (Sanderson 1997, 2003).

Results

Selected shells of *Bythinella* from some of the studied localities are presented in Fig. 2A–Q. It is visible that the variability at one locality (B10: Fig. 2G–Q) is equivalent to the variation observed amongst all populations.

We obtained 58 new sequences of COI (552 bp, GenBank Accession numbers KT381098–KT381155) and 36 new sequences of ITS-1 (234–264 bp, GenBank Accession numbers KT381156–KT381191). For COI the saturation test of Xia et al. (2003) revealed no saturation. Seventeen COI haplotypes (haplotype diversity $H_d = 0.932$) and ten ITS-1 haplotypes ($H_d = 0.837$) were identified. For phylogenetic analyses, additional *Bythinella* sequences available in GenBank (Table 1) were included, including those from eight sites in Bulgaria (15 haplotypes: Falniowski et al. 2009a, 2012), twelve sites in Romania (22 haplotypes: Falniowski et al. 2009b) and five sites in Montenegro (six haplotypes) and Serbia (five haplotypes: Falniowski et al. 2012). The topologies of the resulting ML and BI phylograms were identical. Sequences of *Bythinella viridis* were used as outgroup in all analyses to root the trees.

In the COI trees five main clades could be distinguished for the Bulgarian populations (Figs 3–4). Clade I included the largest number of haplotypes covering an area from the Rhodopes Mts through the Maritsa Valley to the Stara Planina and Sredna Gora Mts. This clade is characterized by a low sequence divergence (p -distance within this group = 0.008, Table 2). The relationships between the haplotypes of this clade are depicted in a haplotype network in Fig. 5. Most haplotypes from this clade belonged to snails inhabiting surface waters while two of them represent cave populations (Fig. 3). This clade represents several nominal species: *B. angelovi*, *B. dierkingi*, *B. gloeeri*, *B.*

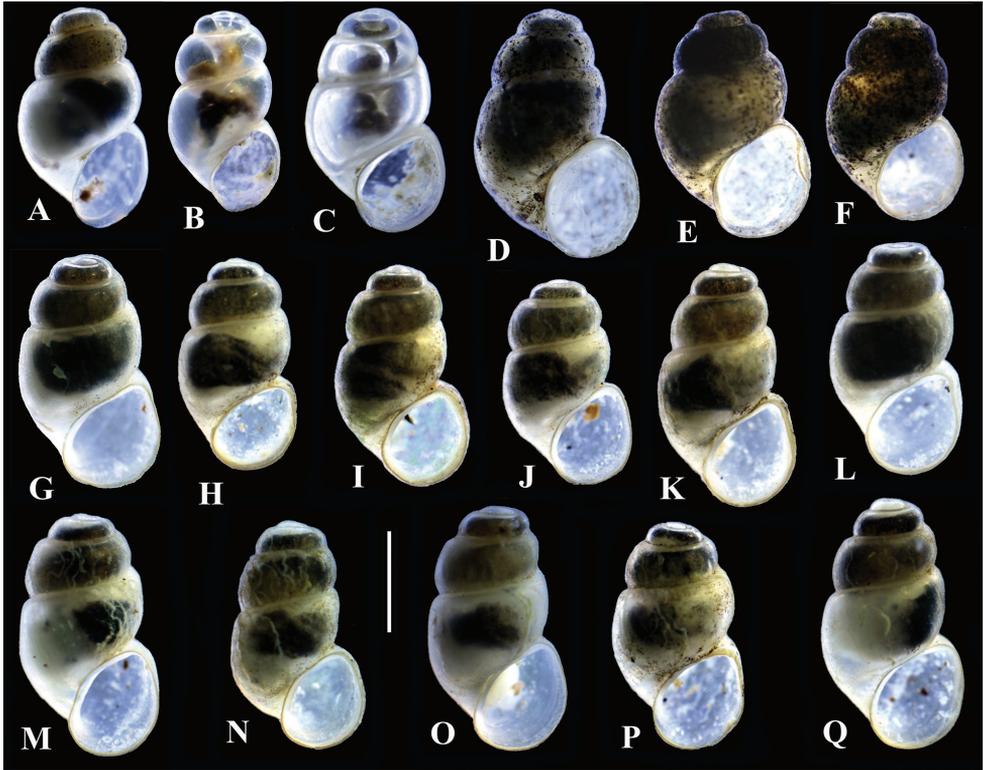


Figure 2. Shells of *Bythinella*. **A** locality B1 **B–C** locality B7 **D–F** locality B5 **G–Q** locality B10; bar equals 1 mm.

Table 2. Mean distances within clades (*italics*) and *p*-distances between main COI clades of *Bythinella*.

	clade_I	clade_II	clade_III	Serbia	clade_IV	Serbia/Mont.	clade_V	Romania
	<i>0.008</i>							
clade_II	0.024	<i>0.002</i>						
clade_III	0.026	0.031	-					
Serbia	0.063	0.070	0.054	<i>0.002</i>				
clade_IV	0.089	0.090	0.078	0.089	-			
Serbia/Mont.	0.109	0.112	0.096	0.119	0.122	<i>0.023</i>		
clade_V	0.091	0.090	0.084	0.090	0.118	0.126	<i>0.004</i>	
Romania	0.112	0.106	0.097	0.120	0.122	0.118	0.109	<i>0.079</i>

hansboetersi, *B. ravnogorica*, *B. rhodopensis*, *B. rilaensis*, *B. slaveyae*, and *B. srednogorica*, in fact based mostly on their locations.

Clades II and III were most closely related to Clade I differing by intercladal *p*-distances of 0.024 and 0.026 and inferred divergence times of 0.82 and 1.89 Mya, respectively (Table 2). Clade II contained haplotypes from two sites in the south-west of Bulgaria: the Pirin Mts and a cave in the Rhodopes Mts, from which *B. stoychevae*

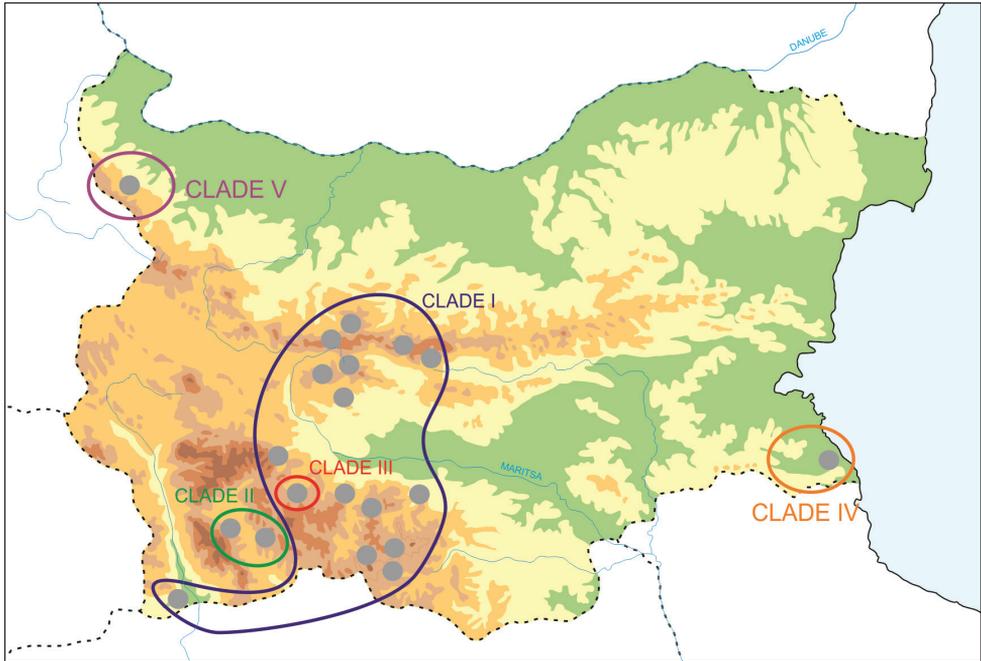


Figure 4. Geographical distribution of COI clades. Compare with Figure 3.

vergence time 4.39 Mya) (Table 2). This clade is situated between the two reference clades from Serbia and Montenegro. The most divergent clade was Clade V (inferred divergence time 7.25 Mya), formed by three haplotypes from the Vodni Pech Cave in north-western Bulgaria.

The reference sequences formed three distinct clades (Fig. 3). First of them represent one population from eastern Serbia, second the populations from western Serbia and Montenegro. Haplotypes from Romania formed another distinct lineage. The level of divergence between haplotypes within this lineage has been much larger than within the other clades.

Unfortunately, due to technical problems, ITS-1 sequences were not available for samples from Clade IV and for the reference populations from Serbia and Montenegro. The ITS-1 tree (Fig. 6) confirmed the distinctiveness of the Bulgarian *Bythinella* from the Romanian ones. Three clades (A, B, C) could be distinguished. In correspondence with the COI tree, Clade C, containing sequences from the population from the Vodni Pech Cave, was found to be the most divergent (similarly as COI haplotypes from this population). Clade A comprised about half of all haplotypes of COI Clade I plus the COI Clade III. Clade B comprised all samples from COI Clade II and the rest of the samples from COI Clade I.

Shells from different clades (Fig. 2) were found to differ in morphology, but no clade-specific shell characters were found. Similar remarks concern both female reproductive organs, and the penes: no clade-specific character states were found.

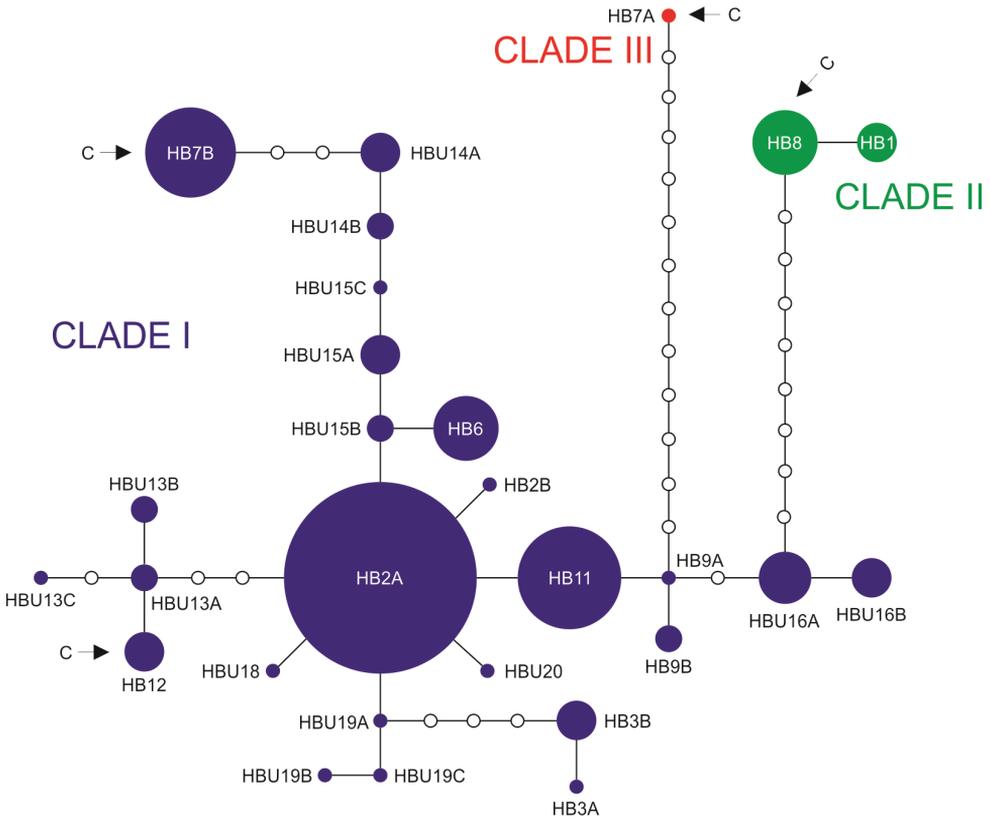


Figure 5. The median-joining haplotype network of COI haplotypes for clades I, II and III. Sequences from Falniowski et al. 2009a and Falniowski et al. 2012 are also included. Arrows and the letter C indicate cave haplotypes.

Discussion

Species delimitation in the genus *Bythinella* remains unclear. New species descriptions were initially based mainly on shell morphology, and on the locality not studied so far. Even for Radoman (1976), whose experience and extensive studies on the truncatelloidean anatomy were a basis for the new taxonomy proposed by him, the shell characters alone were the only basis for species-level taxonomy. He even stated that there could not be any differences in soft part morphology and anatomy between the congeneric species. Later, anatomy, especially of the reproductive system was considered (Boeters 1973, 1998; Falniowski 1987). In many cases, the number of species recognized from different parts in Europe is probably overestimated and the characters traditionally used to delimit species should be re-evaluated (Bichain et al. 2007b). In general, in *Bythinella* it is impossible to distinguish particular species without molecular data (Szarowska and Falniowski 2008; Falniowski et al. 2009b, c; Falniowski and Szarowska 2011). Analysis of the COI genetic distances between recognized clades/

Most populations examined here occurred in the area from the Rhodopes Mts to the Sredna Gora Mts (Clades I, II, III). Only two other isolated populations were found in eastern Bulgaria, in the Strandzha Mts (Clade IV) and in the north-western part of this country (Clade V). Despite an extensive search, no members of this genus were found in the rest of Bulgaria (Fig. 1). However, there are several areas where no *Bythinella* occur, since these snails are sensitive to environmental conditions, such as high water calcium content and low temperature. They occasionally occur in spring outlets and creeks, and also in caves or groundwaters (Giusti and Pezzoli 1977, 1980). Water conditions may be one of the most important factors influencing the occurrence of *Bythinella*. On the one hand, regional and global environmental changes may have relatively small effects on this spring snail, since springs can buffer such changes. On the other hand, *Bythinella* is more resistant than had been expected for a long time (e.g., Szarowska 2000) and, since springs are ephemeral habitats that are certainly not long-lasting, there must be unexpectedly high gene flow between them to colonize/recolonize them (e.g., Falniowski et al. 1998, 1999).

Low, infraspecies-level diversity characterized Clade I, including most of the studied populations distributed across central and western Bulgaria. The representatives of Clades II, III and V either migrated from the west, or survived there from earlier time. It seems possible that both clades III and V survived glaciations inside the caves. Clade IV most probably originated in the present Asia Minor. The closest sequences to clade V come from the *B. turca* haplotype from the Egirdir Lake in Turkey (p distance = 0.055).

Mitochondrial interpopulation differentiation of Bulgarian *Bythinella* (p distance = 0.03) is much smaller than in neighbouring countries (p distance = 0.06–0.08). The greater genetic differences between *Bythinella* populations in Romania have been compared with the surprisingly low differentiation amongst the Bulgarian ones by Falniowski et al. (2009a,b). However, this analysis was only based on a small number of Bulgarian populations. The more detailed sampling in the present work confirmed this phenomenon. Moreover, lower interpopulation differentiation than in the Romanian *Bythinella* was also demonstrated for Greek populations (Falniowski et al. 2011) and throughout the East Balkans (Falniowski et al. 2012).

Within Bulgaria, some geological events could explain the low divergence in Clade I. The Dacic Basin, a vast water body that separated the Carpathians from the recent central Bulgaria before and just after the peak of Messinian Salinity Crisis (5.60–5.46 Mya) (Popov et al. 2004, 2006; Popescu et al. 2009; Suc et al. 2011), was a part of the Paratethys, connected with the Pannonian Basin in the west, the Euxinian Basin in the east, and directly with the present Aegean Sea in the south. Although its water-filled area eventually decreased in size, it was still present until the middle Pleistocene, about 1.8 Mya. The Dacic Basin most probably separated the ancestors of the two large clades, about 8 Mya. Later, in the Pleistocene, the unstable fluviolacustrine system in south-western Bulgaria and northern Greece, with glaciers present in the Pirin and Rila Mts (Zagorchev 2007), probably formed effective, temporary barriers for *Bythinella*, and may have caused its extinction in most of Bulgaria. Considering the data known so far, the small differences among the Bulgarian populations representing Clade I may

reflect the short history of *Bythinella* in the area, which was most probably recolonised from the south, certainly not from the north, no earlier than in the late Pleistocene.

Benke et al. (2011) revealed that genetic diversity of *Bythinella* in Europe is not distributed equally, and identified five “hotspots”: Massif Central and Pyrenees, western Alps and northern Apennines, eastern Alps, western Carpathians and eastern Carpathians. The authors of the present paper discovered another *Bythinella* hotspot in central Greece (Szarowska et al. 2015). Thus, all the hotspots occur in mountain areas, which strongly suggests, that this type of landscape is especially favourable for *Bythinella*.

Moreover, almost all these hotspots are in places that were previously identified as *Bythinella* Pleistocene glacial refugia (Benke et al. 2009; Falniowski et al. 2009b), so high differentiation level in Romania may be the result of glaciations. During the Pleistocene these areas were probably a set of small areas of a nunatak character, with a mild climate suitable for *Bythinella* survival (Falniowski et al. 2009). Habitat fragmentation and subsequent periods of isolation in such shelters must have promoted speciation and could explain high differentiation level. It is widely accepted that, during glacial periods, the Pontic-Mediterranean refugium included territory in present-day Romania (e.g., Falniowski et al. 2009b). It seems that there is no trace of such refugium in Bulgaria.

Caves are relatively stable long-lasting environments and individual ones often have an island character with no subterranean connections to any others. In some cases, particular caves can be characterized by endemic taxa with long, independent, evolutionary histories (e.g., Falniowski et al. 2008, Juan et al. 2010 for references) that differ strongly from their sister taxa occurring outside caves. *Bythinella* inhabits both surface and underground waters, providing thus opportunity to compare populations from those two kind of habitats. In Bulgaria, only clade V was formed by haplotypes clearly distinct from the remaining *Bythinella* populations, which may reflect their troglobiontic character, and longevity of isolation, approaching the Pliocene. The collected individuals were, in fact, found not inside the cave, but at its entrance, in the water running from the cave, but this is normal way of collecting of several troglobiontic gastropods. In this population three haplotypes were found, in COI as well as in ITS-1, which is not common in troglobiontic animals (Juan et al. 2010), whose populations are usually monomorphic. This polymorphism may also confirm the longevity of this population, or inhabiting the cave by more than one species. Clade III was formed by a single COI haplotype from Lepenitza cave, locality B7, and represents *B. gloeri*. This haplotype, originated probably in the Calabrian, Pleistocene, also presents a distinct, probably troglobiontic lineage. In both cases – COI clades V and III, the “climatic relict” hypothesis, as proposed by Howarth 1973 (Holsinger 1988, 2000; Peck and Finston 1993, Rivera et al. 2002). According to this hypothesis, after the colonization of subterranean habitats there still takes place gene flow between the subterranean and surface population, but later, in strict allopatry, the subterranean population still speciates, and the surface population becomes extinct as a result of climatic changes, like glaciations or growing aridity. This seems a typical pattern for temperate climate. It has to be noted, however, that at the same cave there was found another haplotype, belonging to the COI clade I. This is one more example of sympatric occurrence of more

than one *Bythinella*. Such a situation is not unlikely and has been previously reported for *Bythinella* (Radoman 1976; Falniowski et al. 2009b, Falniowski and Szarowska 2011). This haplotype is close to the one inhabiting surface waters at locality B14, situated close to this cave. Similarly, the COI haplotype from troglobiont population at locality B12 (Modarskata Cave) was close to the one from the surface population 13, situated closely to population B12; the same concerns the troglobiont population B8 from Manuilova Dupka Cave compared with surface population B1. Low divergence between those troglobiont populations and their surface relatives may reflect either the early phase of the “climatic relict”-model processes, or “adaptive shift”-model: adaptive evolution of the lineages invading subterranean habitats, coupled with survival of the ancestral population at the surface.

Considering the observed pattern of interpopulation differentiation of *Bythinella* in Bulgaria, the facts listed above, and the divergence time estimates, we could suppose that the isolation between clades I, II and III (0.82 Mya and 1.89 Mya, respectively) may have been caused by subsequent glaciations during the Pleistocene. The time of isolation between the above three clades and clade IV from SE Bulgaria (4.39 Mya) coincides with the Messinian Salinity Crisis. Later, the low level of the present Black Sea promoted migration of the representatives of this clade from Asia Minor to Europe. The distinctness of clade V, found at NW Bulgaria, most probably reflects the isolation of the Rhodopes from the western Balkan Mts by the Dacic Basin (7.25–1.8 Mya).

Acknowledgements

The study was supported by a grant from the National Science Centre (2012/05/B/NZ8/00407) to Magdalena Szarowska. We wish to thank Dr Helen McCombie-Boundry for improving the English and anonymous reviewers and the editor for valuable comments on the text.

References

- Avice JC (2000) Phylogeography. The history and formation of species. Harvard University Press, Cambridge, MA and London.
- Bandelt HJ, Forster P, Röhl A (1999) Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution* 16: 37–48. doi: 10.1093/oxfordjournals.molbev.a026036
- Benke M, Brändle M, Albrecht C, Wilke T (2009) Pleistocene phylogeography and phylogenetic concordance in cold-adapted spring snails (*Bythinella* spp.). *Molecular Ecology* 18: 890–903. doi: 10.1111/j.1365-294X.2008.04073.x
- Benke M, Brändle M, Albrecht C, Wilke T (2011) Patterns of freshwater biodiversity in Europe: lessons from the spring snail genus *Bythinella*. *Journal of Biogeography* 38: 2021–2032. doi: 10.1111/j.1365-2699.2011.02527.x

- Bichain JM, Gaubert P, Samadi S, Boisselier-Dubayle MC (2007a) A gleam in the dark: Phylogenetic species delimitation in the confusing spring-snail genus *Bythinella* Moquin-Tandon, 1856 (Gastropoda: Rissooidea: Amnicolidae). *Molecular Phylogenetics and Evolution* 45: 927–941. doi: 10.1016/j.ympev.2007.07.018
- Bichain JM, Boisselier Dubayle MC, Bouchet P, Samadi S (2007b) Species delimitation in the genus *Bythinella* (Mollusca: Caenogastropoda: Rissooidea): A first attempt combining molecular and morphoetrical data. *Malacologia* 49: 293–311. doi: 10.4002/0076-2997-49.2.293
- Boeters HD (1973) Die Gattung *Bythinella* and Gattung *Marstoniopsis* in Westeuropa, 1. Westeuropäische Hydrobiidae, 4 (Prosobranchia). *Proceedings of Fourth European Malacological Congress. Malacologia* 14: 271–285.
- Boeters HD (1998) Mollusca: Gastropoda: Superfamilie Rissooidea. In: Schwoerbel J, Zwick P (Eds) *Süsswasserfauna von Mitteleuropa. Begründet von A. Brauer, 5/1–2*, Gustav Fischer Verlag, Jena – Lübeck – Ulm.
- Falniowski A (1987) Hydrobioidea of Poland (Prosobranchia: Gastropoda). *Folia Malacologica* 1: 1–122.
- Falniowski A (1992) Shell outer and inner structure and rissocean phylogeny. III. *Truncatella subcylindrica* (Linnaeus, 1767) (Prosobranchia: Rissoacea: Truncatellidae). *Malakologische Abhandlungen, Staatliches Museum für Tierkunde Dresden* 16: 7–11.
- Falniowski A, Horsak M, Szarowska M (2009a) *Bythinella hansboetersi* Glöer et Pešić, 2006 (Gastropoda: Rissooidea) in Bulgaria: its morphology, molecular distinctness, and phylogeography. *Folia Malacologica* 17: 11–20. doi: 10.2478/v10125-009-0002-3
- Falniowski A, Mazan K, Szarowska M (1999) Homozygote excess and gene flow in the spring snail *Bythinella* (Gastropoda: Prosobranchia). *Journal of Zoological Systematics and Evolutionary Research* 37: 165–175. doi: 10.1111/j.1439-0469.1999.tb00980.x
- Falniowski A, Szarowska M, Fiałkowski W, Mazan K (1998) Unusual geographic pattern of interpopulation variation in a spring snail *Bythinella* (Gastropoda, Prosobranchia). *Journal of Natural History* 32: 605–616. doi: 10.1080/00222939800770311
- Falniowski A, Szarowska M, Sirbu I (2009b) *Bythinella* Moquin-Tandon, 1856 (Gastropoda: Rissooidea: Bythinellidae) in Romania: species richness in a glacial refugium. *Journal of Natural History* 43: 2955–2973. doi: 10.1080/00222930903359636
- Falniowski A, Szarowska M, Sirbu I (2009c) *Bythinella* Moquin-Tandon, 1856 (Gastropoda: Rissooidea: Bythinellidae) in Romania: its morphology with description of four new species. *Folia Malacologica* 17: 21–36. doi: 10.2478/v10125-009-0003-2
- Falniowski A, Szarowska M (2011) Radiation and phylogeography in a spring snail *Bythinella* (Mollusca: Gastropoda: Rissooidea) in continental Greece. *Annales Zoologici Fennici* 48: 67–90. doi: 10.5735/086.048.0201
- Falniowski A, Szarowska M (2012) Sequence-based species delimitation in the Balkan *Bythinella* Moquin-Tandon, 1856 (Gastropoda: Rissooidea) with general mixed Yule coalescent model. *Folia Malacologica* 20: 111–120. doi: 10.2478/v10125-012-0017-z
- Falniowski A, Szarowska M, Sirbu I, Hillebrand A, Baciu M (2008) *Heleobia dobrogica* (Grossu & Negrea, 1989) (Gastropoda: Rissooidea: Cochliopidae) and the estimated time of its isolation in a continental analogue of hydrothermal vents. *Molluscan Research* 28: 165–170.

- Falniowski A, Szarowska M, Glöer P, Pešić V, Georgiev D, Horsák M, Sirbu I (2012) Radiation in *Bythinella* Moquin-Tandon, 1856 (Mollusca: Gastropoda: Rissooidea) in the Balkans. *Folia Malacologica* 20: 1–10. doi: 10.2478/v10125-012-0006-2
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek RC (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299.
- Georgiev D (2009) *Bythinella gloeeri* n. sp. – a new cave inhabiting species from Bulgaria (Gastropoda: Rissooidea: Hydrobiidae). *Acta Zoologica Bulgarica* 61: 223–227.
- Georgiev D (2011) New species of snails (Mollusca: Gastropoda: Rissooidea) from cave waters of Bulgaria. *Buletin Shkencor, ser. Shkencat Natyrore [Universiteti i Shkodrës “Luigi Gurakuqi”]* 61: 83–96.
- Georgiev D, Glöer P (2013) Identification key of the Rissooidea (Mollusca: Gastropoda) from Bulgaria with a description of six new species and one new genus. *North-Western Journal of Zoology* 9: 103–112.
- Georgiev D, Stoycheva S (2008) A record of *Bythinella* cf. *opaca* (Gallenstein, 1848) (Gastropoda: Prosobranchia: Hydrobiidae) in Bulgaria. *Malacologica Bohemoslovaca* 7: 51–54.
- Giusti F, Pezzoli E (1977) Primo contributo alla revisione del genere *Bythinella* in Italia. *Natura Bresciana, Annuario del Museo Civico di Storia Naturale di Brescia* 14: 3–80.
- Giusti F, Pezzoli E (1980) Gasteropodi, 2 (Gastropoda: Prosobranchia; Hydrobioidea, Pyrguloidea). In: *Collana del progetto finalizzato “Promozione della qualità dell’ambiente,” AQ/1/47. Guide per il riconoscimento delle specie animali delle acque interne Italiane* 8. Consiglio Nazionale delle Ricerche, Verona, 1–67.
- Glöer P, Georgiev D (2009) New Rissooidea from Bulgaria (Gastropoda: Rissooidea). *Mollusca* 27: 123–136.
- Glöer P, Georgiev D (2011) Bulgaria, a hot spot of biodiversity (Gastropoda: Rissooidea)? *Journal of Conchology* 40: 1–16.
- Glöer P, Pešić V (2006) *Bythinella hansboetersi* n. sp., a new species from Bulgaria. *Heldia* 6: 11–15.
- Haase M, Wilke T, Mildner P (2007) Identifying species of *Bythinella* (Caenogastropoda: Rissooidea): A plea for an integrative approach. *Zootaxa* 1563: 1–16.
- Holsinger JR (1988) Troglobites: the evolution of cave-dwelling organisms. *American Scientist* 76: 146–153.
- Holsinger JR (2000) Ecological derivation, colonisation and speciation. In: Wilkens H, Culver D, Humphreys W (Eds) *Subterranean Ecosystems*. Elsevier, Amsterdam, 399–415.
- Howarth FG (1973) The cavernicolous fauna of Hawaiian lava tubes. I. Introduction. *Pacific Insects* 15: 139–151.
- Huelsenbeck JP, Rannala B (2004) Frequent properties of Bayesian posterior probabilities of phylogenetic trees under simple and complex substitution models. *Systematic Biology* 53: 904–913. doi: 10.1080/10635150490522629
- Juan C, Guzik MT, Jaume D, Cooper SJB (2010) Evolution in caves: Darwin’s ‘wrecks of ancient life’ in the molecular era. *Molecular Ecology* 19: 3865–3880. doi: 10.1111/j.1365-294X.2010.04759.x
- Librado P, Rozas J (2009) DnaSP v5 a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics* 25: 1451–1452. doi: 10.1093/bioinformatics/btp187

- Mazan K (2000) Morphologica and allozymic variation within and between populations of *Bythinella* Moquin-Tandon, 1855 (Gastropoda: Prosobranchia). I. Morphological characters. *Folia Malacologica* 8: 107–139. doi: 10.12657/folmal.008.007
- Mazan K, Szarowska M (2000a) Morphologica and allozymic variation within and between populations of *Bythinella* Moquin-Tandon, 1855 (Gastropoda: Prosobranchia). II. Phe-netic analysis. *Folia Malacologica* 8: 189–213. doi: 10.12657/folmal.008.014
- Mazan K, Szarowska M (2000b) Morphologica and allozymic variation within and between populations of *Bythinella* Moquin-Tandon, 1855 (Gastropoda: Prosobranchia). III. Phylo-genetic analysis. *Folia Malacologica* 8: 257–269. doi: 10.12657/folmal.008.022
- Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov., New Orleans, LA, 1–8. doi: 10.1109/gce.2010.5676129
- Nei M, Kumar S (2000) *Molecular Evolution and Phylogenetics*. Oxford University press, Oxford, UK and New York.
- Peck SB, Finston TL (1993) Galapagos islands troglobites: the questions of tropical troglobites, parapatric distributions with eyed-sister-species, and their origin by parapatric speciation. *Memoires de Biospielologie* 20: 19–37.
- Popescu S-M, Dalesme F, Jouannic G, Escarguel G, Head M, Melinte-Dobrinescu M-C, Sütö-Szentai M, Bakrac K, Clauzon G, Suc JP (2009) *Galeacysta etrusca* complex: dinoflagellate cyst marker of Paratethyan influxes to the Mediterranean Sea before and after the peak of the Messinian Salinity Crisis. *Palynology* 33: 105–134. doi: 10.1080/01916122.2009.9989688
- Popov SV, Rögl F, Rozanov AY, Steininger FF, Shcherba IG, Kovac M (2004) Lithologi-cal-paleogeographic maps of the Paratethys. 10 maps Late Eocene to Pliocene. *Courier Forschungsinstitut Senckenberg* 250: 1–46.
- Popov SV, Shcherba IG, Ilyina LB, Nevesskaya LA, Paramonova NP, Khondkarian SO, Magyar I (2006) Late Miocene to Pliocene palaeogeography of the Paratethys and its relation to the Mediterranean. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238: 91–106. doi: 10.1016/j.palaeo.2006.03.020
- Radoman P (1976) Speciation within the family Bythinellidae on the Balkans and Asia Mi-nor. *Zeitschrift für Zoologische Systematik und Evolutionsforschung* 14: 130–152. doi: 10.1111/j.1439-0469.1976.tb00522.x
- Rivera MAJ, Howarth FG, Taiti S, Roderick GK (2002) Evolution in Hawaiian cave isopods (Oniscidea: Philosciidae): vicariant speciation or adaptive shifts? *Molecular Phylogenetics and Evolution* 25: 1–9. doi: 10.1016/S1055-7903(02)00353-6
- Ronquist F, Teslenko M, van der Mark P, Ayres D, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic infer-ence and model choice across a large model space. *Systematic Biology* 61: 539–542. doi: 10.1093/sysbio/sys029
- Sanderson MJ (1997) A nonparametric approach to estimating divergence times in the absence of rate constancy. *Molecular Biology and Evolution* 14: 1218–1231. doi: 10.1093/oxford-journals.molbev.a025731

- Sanderson MJ (2003) R8s: inferring absolute rates of molecular evolution, divergence times in the absence of a molecular clock. *Bioinformatics* 19: 301–302. doi: 10.1093/bioinformatics/19.2.301
- Suc J-P, Do Couto D, Carmen Melinte-Dobrinescu M, Macaieș R, Quillévéré F, Clauzon G, Csato I, Rubino J-L, Popescu S-M (2011) The Messinian Salinity Crisis in the Dacic Basin (SW Romania) and early Zanclean Mediterranean-Paratethys high sea-level connection. *Palaeogeography, Palaeoclimatology, Palaeoecology* 310: 256–272. doi: 10.1016/j.palaeo.2011.07.018
- Stamatakis A (2014) RAxML Version 8: A tool for Phylogenetic Analysis and Post-Analysis of Large Phylogenies. *Bioinformatics* 30: 1312–1313. doi: 10.1093/bioinformatics/btu033
- Szarowska M (2000) Environmental stress and stability of *Bythinella* populations in South Poland (Gastropoda: Prosobranchia: Hydrobioidea). *Malakologische Abhandlungen* 20: 93–98.
- Szarowska M, Falniowski A (2008) There is no philosopher's stone: *coup de grace* for the morphology-based systematics in the rissooidean gastropods? 5th Congress of the European Malacological Societies, Ponta Delgada, 28.
- Szarowska M, Osikowski A, Hofman S, Falniowski A (2015) Do diversity of the spring-inhabiting snail *Bythinella* (Gastropoda, Bythinellidae) on the Aegean Islands reflect geological history? *Hydrobiologia*. doi: 10.1007/s10750-015-2415-x
- Tajima F (1993) Simple methods for testing molecular clock hypothesis. *Genetics* 135: 599–607.
- Tamura K, Stecher G, Peterson D, Filipski A, Kumar S (2013) MEGA6: Molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution* 30: 2725–2729. doi: 10.1093/molbev/mst197
- Wilke T, Davis GM (2000) Intraspecific mitochondrial sequence diversity in *Hydrobia ulvae* and *Hydrobia ventrosa* (Hydrobiidae: Rissoacea: Gastropoda): Do their different life histories affect biogeographic patterns and gene flow? *Biological Journal of the Linnean Society* 70: 89–105. doi: 10.1111/j.1095-8312.2000.tb00202.x
- Xia X (2013) DAMBE: A comprehensive software package for data analysis in molecular biology and evolution. *Molecular Biology and Evolution* 30: 1720–1728. doi: 10.1093/molbev/mst064
- Xia X, Xie Z, Salemi M, Chen L, Wang Y (2003) An index of substitution saturation and its application. *Molecular Phylogenetics and Evolution* 26: 1–7. doi: 10.1016/S1055-7903(02)00326-3
- Zagorchev I (2007) Late Cenozoic development of the Strouma and Mesta fluviolacustrine systems, SW Bulgaria and northern Greece. *Quaternary Science Reviews* 26: 2783–2800. doi: 10.1016/j.quascirev.2007.07.017

Checklist of tortoise beetles (Coleoptera, Chrysomelidae, Cassidinae) from Colombia with new data and description of a new species

Lech Borowiec¹, Jolanta Świątojańska¹

¹ Department of Biodiversity and Evolutionary Taxonomy, University of Wrocław, Przybyszewskiego 63/77, 51-148 Wrocław, Poland

Corresponding author: *Lech Borowiec* (lech.borowiec@uwr.edu.pl)

Academic editor: *C. Chaboo* | Received 6 February 2015 | Accepted 13 August 2015 | Published 25 August 2015

<http://zoobank.org/9CC9B00B-A497-4307-88F2-FDAD7B87A311>

Citation: Borowiec L, Świątojańska J (2015) Checklist of tortoise beetles (Coleoptera, Chrysomelidae, Cassidinae) from Colombia with new data and description of a new species. ZooKeys 518: 87–127. doi: 10.3897/zookeys.518.9350

Abstract

A new tortoise beetle species, *Cyrtanota abrili*, is described from the Antioquia and Caldas departments in Colombia. New faunistic data are provided for 87 species, including 16 new additions to the country's fauna. A checklist of the known 238 species of tortoise beetles recorded from Colombia is given.

Keywords

Coleoptera, Chrysomelidae, Cassidinae, *Cyrtanota abrili*, new faunistic data, checklist, Colombia

Introduction

Colombian tortoise beetles [Coleoptera, Chrysomelidae, Cassidinae, in the new sense excl. the tribes Cephaloleiini (= Imatidiini) and Spilophorini] (Borowiec 1995, Staines 2002, Sekerka 2014) are poorly known because most data are devoted to original descriptions of new taxa and no regional catalogues or checklists have been published (Borowiec and Świątojańska 2014b). Although 221 species were recorded from the country hitherto, most of them have been noted without precise location or even province name (Borowiec 1999). The most recent data of several dozen species were pub-

lished by Borowiec (1996, 2002a, 2009b) based on materials from various museums and private collections but outside Colombian institutions. Recently, we had the opportunity to study specimens preserved in the Museo Entomológico UNAB, Universidad Nacional de Colombia, Bogotá. The collection includes specimens representing 87 species of tortoise beetles, including one species new to science and 16 species new to the country. The material was collected in the last fifty years and most specimens are well-labeled with department and locality data, including geographical coordinates. In this paper we describe this new species of *Cyrtonota* Chevrolat, 1837, after reviewing the material preserved in the Museo Entomológico UNAB, Universidad Nacional de Colombia, Bogotá, and provide a checklist of 238 species of tortoise beetles known from Colombia, including department data for each taxon, when available.

Methods

Taxa in the faunistic list below are arranged alphabetically, by tribe, genus and species. Geographical coordinates are in DMS format. The new species was identified to the genus *Cyrtonota* based on previous studies (Borowiec 2007a, 2009a; Sekerka 2007) that examined all the other known species.

Photos were taken using Nikon SMZ 1500 stereomicroscope with Nikon Coolpix 4500 photo camera as several separate layers and combined in the Helicon Focus software. Exact label data are cited for type material. A forward slash (/) separates different lines.

Description of a new species

Cyrtonota abrili Borowiec & Świętojańska, sp. n.

<http://zoobank.org/84D93316-606F-4FC4-9E7B-2A307D0C5B65>

Type locality. Colombia, Antioquia department, Envigado city, El Salado quarter, 1573 m a.s.l.

Type material. Holotype: “Colombia, Antioquia, / Envigado El Salado / 1.573 m alt. / En: Maleza Oct-1991 / G. Abril R.”; two reticulate paratypes: the same data; spotted paratype “Colombia, Antioquia, / La Estrella 1.764 m alt. / En: *Piperus* sp. / Abr-1985 V.A. Cortés M.”; spotted paratype: “Colombia, Caldas, / Versalles / En: *Pinnus patula* / Jun-1991 G. Abril R.” (holotype and three paratypes preserved in the Museo Entomológico UNAB, Universidad Nacional de Colombia, Bogotá, Colombia, one paratype in the Department of Biodiversity and Evolutionary Taxonomy, Zoological Institute, University of Wrocław, Wrocław, Poland).

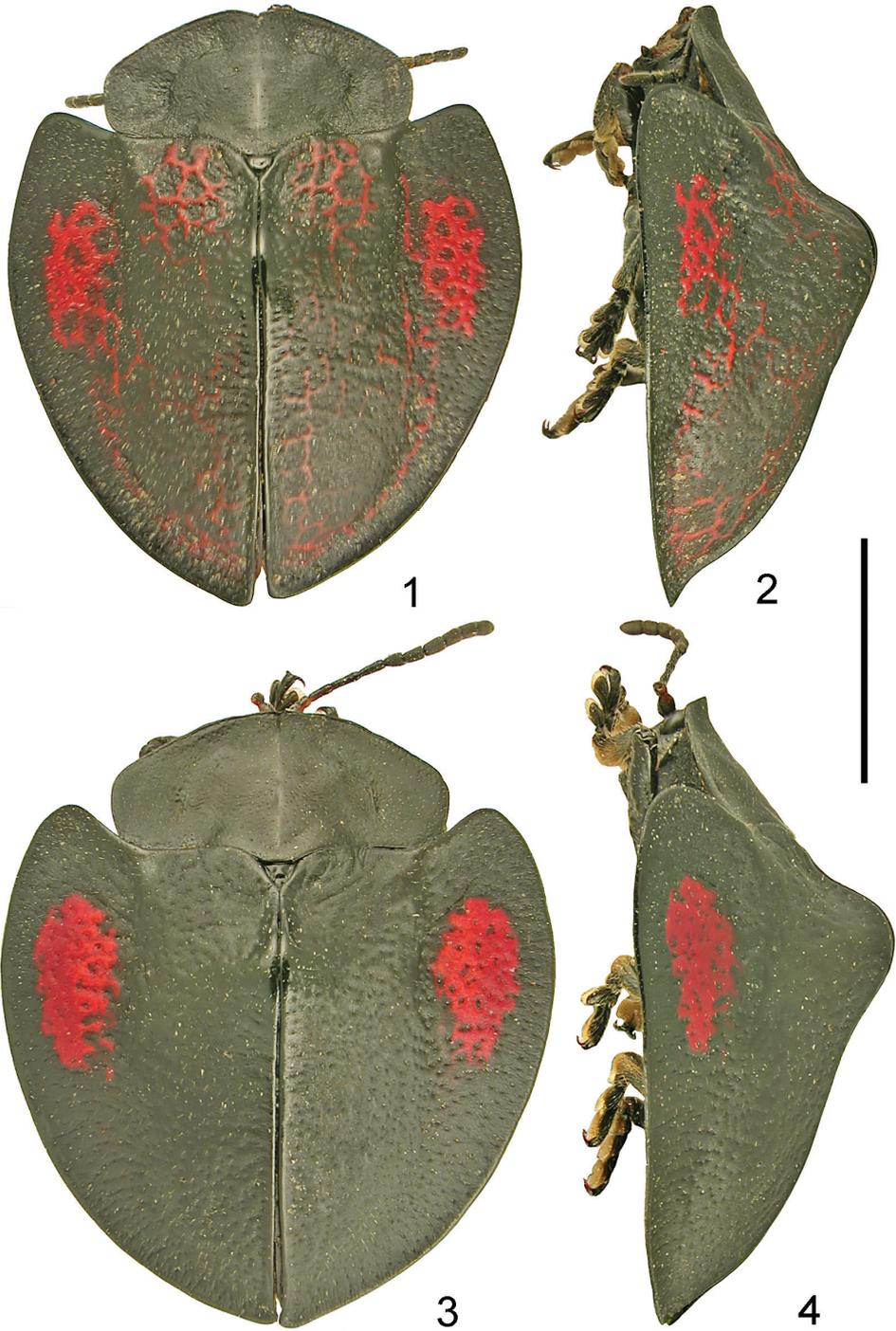
Diagnosis. Black antennae, rounded basal pronotal angles, large scutellum, indistinct sexual dimorphism, venter of pronotum without antennal grooves, short last segment of tarsi, short prosternal collar, antennae with five basal glabrous segments and antennomeres 4 and 5 approximately as long as antennomere 3 place this species

in the genus *Cyrtanota*. *Cyrtanota abrili* belongs to the group of species with dorsum without metallic tint. The group was keyed by Borowiec (2007a, with a modification in 2009a) and characters of *C. abrili* lead to the couplet 13:

- 13 Pronotum with two spots of extremely dense vestiture..... **14**
- Pronotum without spots of extremely dense vestiture **16**
- 14 Suture and humeral calli partly or completely black..... 15
- Suture and humeral calli the same colour as rest of elytra, fulvous to brown. Peru..... ***C. caprishensis* Sekerka**
- 15 Pronotum almost semicircular. Ground colour of elytra paler, yellowish-brown. Suture completely black. Basal antennal segments yellowish ventrally. Colombia..... ***C. lurida* (Spaeth)**
- Pronotum subtrapezoidal. Ground colour of elytra darker, brown. Suture only in anterior part black. Antennae uniformly black. Ecuador ***C. aurovestita* (Spaeth)**
- 16 Elytra with red reticulation or with red reticulate spots..... **17**
- Elytra without red reticulation or red reticulate spots..... **20**
- 17 Elytra on whole surface with red reticulation 18
- Elytra with red irregular spots or only partly with red reticulation **17a**
- 17a Elytra, on both, disc and explanate margin with irregular reticulation or only explanate margin with large, red, irregular spot. Colombia **17b**
- Elytra with six red reticulate spots: two in postscutellar impression, one in the middle of margin of disc and two on slope. Brazil: Bahia... ***C. bondari* (Spaeth)**
- 17b Pronotum more transverse, length/width ratio 2.34. Body stouter, approximately as long as wide, elytral disc forms almost regular, very high gibbosity, punctuation of disc very coarse, punctures mostly touching each other, red spot on explanate margin almost round. Colombia ***C. pyramidata* (Boheman)**
- Pronotum less transverse, length/width ratio 1.85–1.97. Body slimmer, longer than wide, elytral disc with high gibbosity in postscutellar area but less convex after the gibbosity, punctuation of disc fine, distance between punctures mostly three to four times wider than puncture diameter, red spot on explanate margin elongate. Colombia ***C. abrili* sp. n.**

Description. Holotype: length 12.4 mm, width 10.6, length of pronotum 3.3 mm, width of pronotum 6.4 mm, length/width ratio 1.17, width/length ratio of pronotum 1.94; paratypes: length 11.3–13.7 mm, width 10.4–13.2 mm, length of pronotum 3.4–3.7 mm, width of pronotum 6.3–7.2 mm, length/width ratio 1.04–1.14, width/length ratio of pronotum 1.85–1.97. Body stout, elytra regularly rounded on sides, apex of elytra angulate but not elongate or acuminate (Figs 1, 3).

Pronotum and scutellum black. Ground colour of elytra black, in holotype and two paratypes disc with red reticulation in postscutellar impressions, along posterior half of suture and along posterior half of lateral margin of disc, and explanate margin of elytra in anterior third with large red, reticulate spot (Fig. 1); in two other paratypes



Figures 1–4. *Cyrtanota abрили* sp. n. **1** holotype dorsal **2** holotype lateral **3** paratype dorsal **4** paratype lateral. Scale bar: 5 mm.

elytral disc completely black and explanate margin of elytra in anterior third with large red spot without reticulation but with irregular borders and few dark punctures (Fig. 2). Head, antennae, legs and ventrites uniformly black, sometimes last sternite on sides with small, transverse, yellowish-brown spot.

Pronotum transverse, with maximum width approximately in the middle, sides broadly rounded, anterior margin straight or with small triangular emargination in the middle. Surface of disc dull with thin, partly shiny, median, longitudinal line and fine, shallow and very sparse punctation, distance between punctures many times wider than puncture diameter. Explanate margin of pronotum distinctly bordered from disc, on sides with short but deep impression, surface dull, similarly punctate as disc, in some specimens with fine irregular wrinkles.

Scutellum small, triangular, without transverse groove. Base of elytra much wider than pronotum, humeri moderately protruding anterad, humeral angles rounded. Disc very convex, with large but obtuse postscutellar tubercle (Figs 2, 4). Surface in reticulate specimens with thin red reticulation in postscutellar impressions partly extending to latero-basal parts of elytral tubercle, thin red reticulation along both sides of suture and along posterior part of sides of disc, the lateral reticulation joined with red reticulate spot on explanate margin. In dark specimens elytral disc without red reticulation. Dark surface of disc in dark specimens regular, in reticulate specimens slightly irregular with fine and very sparse punctation, dull, distance between punctures mostly three to four times wider than puncture diameter. Whole surface of disc covered with sparse erect setae. Explanate margin of elytra in widest part as wide as half width of disc, in reticulate specimens in anterior third with large, oval, red reticulate spot. In dark specimens the spot is mostly solid, only with irregular margin and several dark punctures but not appears distinctly reticulate. Dark surface of explanate margin regular, dull, punctate similarly as disc. Apex of elytral epipleura without erect hairs.

Ventrites typical for the genus *Cyrtanota*, without diagnostic characters. Genitalia not dissected, in the genus *Cyrtanota* male genitalia are not diagnostic, and spermathecae are not diagnostic within genera of the tribe Mesomphaliini (Borowiec and Opalińska 2007 and unpublished data).

Etymology. Named after the collector, G. Abril, of four of the five specimens of the type series.

Distribution. Antioquia and Caldas departments of north-western Colombia.

Ecology. Little known. The holotype was collected from undergrowth, one paratype on *Piper* sp. and another paratype on *Pinus patula* Schiede ex Schldtl. & Cham. but these plants are unlikely to be the true hosts because the genus *Cyrtanota* is associated with Convolvulaceae plants as far as is known (Borowiec and Świętojańska 2014).

Remarks. *Cyrtanota abrili* is easy to identify using the key presented above. Specimens with red reticulation can be misidentified with small specimens of *Cyrtanota pavens* (Spaeth), and maculate specimens of the new species at first glance are similar to *Cyrtanota deliciosa* (Baly) but both relatives belong to the group of species with elongate or acuminate apex of elytra (couplets 2–12 in Borowiec's (2007a) key) and both are distinctly larger with length 14–19 mm; *C. pavens* differs also in elytra with-

out erect setae. We treated both reticulate and maculate forms as variability of a single species because similar polymorphism is observed in other reticulate Andean *Cyrtanota* and *Stolas* species i.e. *Cyrtanota bergeali* Borowiec & Sassi, *Stolas cruentata* (Erichson) or *Stolas pellicula* (Spaeth). Other characters such as general body shape, size, punctuation, sculpture of surface, vestiture, shape of pronotum, and elytral convexity are the same in both forms.

New faunistic data

Acromis sparsa (Boheman, 1854)

Antioquia, Carepa, Granja Tulenapa, 28 m, 7°46'00"N/76°39'58"W, 13 IX 2001, 1 ex., R. Delgado; **Cundinamarca**, Guaduas, 1007 m, 5°04'12"N/74°35'52"W, 14 X 1995, 1 ex., S. Sánchez; **Cundinamarca**, Vega, 1215 m, 4°59'57"N/74°20'23"W, 8 VII 1976, 1 ex., F. García; **Norte de Santander**, Cúcuta, 320 m, 7°53'N/72°30'W, 13 VI 1975, 1 ex., J. Yañez; **Santander**, La Belleza, Vrda. Los Naranjos, 1900 m, 5°51'57"N/73°58'02"W, 21 III 1997, 1 ex., H. Marin; **Tolima**, Flandes, 290 m, 4°17'N/74°49'W, 27 III 1975, 1 ex., A. Mendoza; **Tolima**, Mariquita, 328 m, 5°12'N/74°55'W, 9 VI 1972, 1 ex., M. Villamizar, 10 VI 1972, 2 ex., F. Mora.

Distribution. Bolivia; Brazil; Colombia; Costa Rica; southern Mexico; Nicaragua; Panama; Peru; Venezuela.

Agroiconota judaica (Fabricius, 1781)

Antioquia, Cocorná, 1288 m, 6°03'25"N 75°11'07"W, VI 1977, 1 ex., R. Vélez; **Antioquia**, Concepción, 1862 m, 6°23'55"N/75°15'22"W, II 1997, 1 ex., F.J. Serna & J.G. Hurtado; **Antioquia**, Fredonia, 1317 m, 5°55'28"N/75°40'51"W, VIII 1985, 1 ex., P.E. Mejía; **Antioquia**, Medellín, 1486 m, 6°13'N/75°34'W, IX 1963, 1 ex., F. Gallego; **Antioquia**, Puerto Triunfo, Rio Claro, 115 m, 5°52'N/74°38'W, V 1985, 1 ex., A. Madrigal; **Antioquia**, Sabaneta, 1609 m, 6°09'11"N, 75°17'19"W, 17 VII 1968, 1 ex., G. Bustamante; **Boyacá**, Turmequé, 2404 m, 5°19'48"N/73°29'42"W, 10 IX 1995, 1 ex., T. Corredor; **Córdoba**, Ayapel, 22 m, 8°19'N, 75°09'W, 1 IV 1969, 1 ex., 4 IV 1969, 1 ex., 12 VI 1969, 1 ex., R. Abisambra; **Cundinamarca**, Agua de Dios, San Marcos, 600 m, 4°22'N/74°40'W, 10 III 2003, 1 ex., L. Moreno & F. Escobar; **Cundinamarca**, Caqueza, Girón de Blanco, 1740 m, 4°24'N/73°53'W, 15 IX 2003, 1 ex., F. Rodríguez; **Cundinamarca**, Fomeque, 1895 m, 4°29'22"N/73°53'54"W, 4 III 2005, 1 ex., N. Rojas; **Cundinamarca**, Fusagasugá, 1746 m, 4°20'49"N/74°21'53"W, I 1980, 1 ex., C. Rojas; **Cundinamarca**, Guayabetal, 1200 m, 4°13'N/73°48'W, 1 V 1969, 1 ex., L.M. Rico & C. Cujía, VI 1969, 1 ex., A. Uribe; **Cundinamarca**, Guayabetal, Vrda. Susumaco, ribera del Rio Negro, 1200 m, 4°13'40"N/73°48'59"W, 11 IV 1993, 1 ex., A. Diego; **Cundinamarca**, Guayabetal de Siquima, 1630 m, 4°52'N/74°28'W, 1

V 1969, 1 ex., A. Silva; **Cundinamarca**, La Mesa, 1298 m, 4°38'05"N, 74°27'57"W, 27 X 1996, 1 ex., S. Olarte; **Cundinamarca**, La Mesa, Laguna Pedro Palo, 1298 m, 4°38'05"N, 74°27'57"W, 13 IX 1997, 1 ex., C. Bejarano, J. Diaz & E. Guzmán; **Cundinamarca**, La Palma, 1462 m, 5°21'51"N/74°23'51"W, 1 ex., A. Pinilla; **Cundinamarca**, Quétame, 1531 m, 4°19'N/73°50'W, VIII 1961, F. Gallego; **Cundinamarca**, Sasaima, 1225 m, 4°57'N/76°26'W, 20 X 1971, 1 ex., A. Coronel; **Cundinamarca**, Usme, 2960 m, 4°28'24"N/74°07'44"W, 8 X 1995, 1 ex., T. Corredor; **Cundinamarca**, Villeta, 842 m, 5°00'52"N/74°28'23"W, 16 III 1968, 1 ex., J. Quintero, 10 XI 2003, 1 ex. G. Herrera; **Cundinamarca**, Viotá, 567 m, 4°26'31"N/74°31'33"W, 20 VII 1976, 5 exx., J. López; **Cundinamarca**, Viotá, El Triunfo, 567 m, 4°26'N/74°31'W, 11 IV 1997, 1 ex., M. Mora; **Meta**, Cubarral, San Luis de Cubarral, Brisas del Ariari, 180 m, 3°47'N/73°52'W, 6 IV 2004, 1 ex., L. Ramirez & A. Vargas; **Meta**, La Macarena, 3°11'16"N/73°45'59'20"W, 10 IX 1996, 1 ex., O. Trujillo; **Meta**, Lejanias, 1000 m, 3°30'49"N/74°03'06"W, 15 V 1994, 1 ex., Peña & Martinez; **Meta**, Puerto Gaitán, 149 m, 4°19'04"N/72°03'17"W, 15 IX 2001, 1 ex., M. Rozo, 26 V 2005, 1 ex., J. Castro; **Meta**, Villavicencio, 467 m, 4°09'N/73°39'W, 10 V 1972, 1 ex., E. Daza, 22 VI 1974, 1 ex., E. Torres, 1 X 1975, 1 ex., O. Rodriguez, 15 VI 1979, 1 ex., W. Guevara, 8 XI 2002, 1 ex., J. Rodriguez, 500 m, 6 X 2003, 1 ex., J. Rodriguez; **Meta**, Villavicencio, Rio Tigre, 467 m, 4°09'N/73°39'W, 21 XI 2003, 1 ex., A. Molano; **Tolima**, Honda, 229 m, 5°12'25"N/74°44'28"W, 15 VI 1971, 1 ex., L. Diaz; **Tolima**, Purificación, 310 m, 3°51'N/74°56'W, 9 IV 1972, 1 ex., D. Bonilla; **Valle del Cauca**, Caicedonia, 1000 m, 4°19'N, 75°50'W, 17 X 2001, 1 ex., C.M. Ospina; **Valle del Cauca**, Miranda, 1111 m, 3°15'19"N/76°13'54"W, 20 VI 1976, 1 ex., H. Durán.

Distribution. Bolivia; Brazil; Colombia; Costa Rica; Ecuador; French Guyana; Guyana; Nicaragua; Panama; Paraguay; Peru; Surinam; Trinidad and Tobago; Venezuela.

Agroiconota propinqua (Boheman, 1855)

Antioquia, Rionegro, 2137 m, 6°09'20"N, 75°22'58"W, 4 IV 1977, 1 ex., L. Zapata; **Caldas**, La Dorada, 178 m, 5°27'N/74°40'W, 11 XII 1965, 1 ex., Pieschacon; **Casanare**, Yopal, 350 m, 5°21'N/72°24'W, 12 X 2003, 1 ex., N. Pachón & R. Ospinañ; **Chocó**, Titumate, 12 m, 8°18'N/77°04'W, IV 1980, 1 ex., E. Urueta; **Cundinamarca**, Agua de Dios, 552 m, 4°22'04"N/74°40'26"W, 2 X 1998, 1 ex., S. Serna; **Cundinamarca**, Anapoima, 698 m, 4°33'18"N/74°32'13"W, 20 XI 1993, 1 ex., P. Numpaque; **Cundinamarca**, Apulo, 421 m, 4°31'18"N/74°35'58"W, 7 IV 1968, 1 ex., F. Santacruz, 4 III 1981, 1 ex., M. Ortega & G. Cavalier; **Cundinamarca**, Bogotá, 2620 m, 4°35'56"N/74°04'51"W, 14 III 1981, 1 ex., 19 XI 1981, 1 ex., Vargas; **Cundinamarca**, Cachipay, Insp. Pol. Anolaima, 5°16'22"N/74°34'22"W, 13 III 1991, 1 ex., G. Castiblanco; **Cundinamarca**, Fusagasugá, 1746 m, 4°20'N/74°21'W, 8 V 1975, 1 ex., R. Puentes; **Cundinamarca**, Girardot, 281 m, 4°18'18"N/74°48'08"W, 12 X 1992, 1 ex., A. Escobar; **Cundinamarca**, Guayabetal, 1200 m, 4°13'40"N/73°48'59"W, 15 III 1969, 1 ex., P. Corzo, 24 VI 1973, 1 ex., R. Madero, 13 V 1974, 1 ex., C. Sierra; **Cun-**

dinamarca, La Mesa, 1298 m, 4°38'05"N, 74°27'57"W, 19 IX 2003, 1 ex., M. Pinzón; **Cundinamarca**, La Mesa, Laguna Pedro Palo, 1298 m, 4°38'05"N, 75°11'7"W, 21 XI 1997, 1 ex., M. Camargo; **Cundinamarca**, La Vega, 1215 m, 4°59'N/74°20'W, 15 V 1996, 1 ex., J. Ardila; **Cundinamarca**, Tena, 1384 m, 4°39'33"N/74°23'28"W, 18 VIII 1998, 1 ex., S. Serma; **Cundinamarca**, Tocaïma, 400 m, 4°27'40"N/74°38'10"W, 8 V 1972, 1 ex., Valero & Saldaña, 23 III 1994, 1 ex., N. Pinzón; **Cundinamarca**, Villeta, 842 m, 5°00'52"N/74°28'23"W, 23 V 1968, 1 ex., A. Duarte; **Magdalena**, Pivijai, 7 m, 10°27'N/74°36'W, VI 1985, 3 ex., A. Madrigal; **Meta**, Villavicencio, 467 m, 4°09'N/73°39'W, 20 VI 1967, 1 ex., E. Peralta; **Tolima**, Ambalema, 285 m, 4°47'N/74°46'W, 17 III 1983, 1 ex., Franco & Rodríguez; **Tolima**, Guamo, 323 m, 4°02'05"N/74°58'25"W, 10 V 1994, 1 ex., M. Peñafort; **Tolima**, Ibagué, 1285 m, 4°26'N/75°14'W, 6 V 1998, 1 ex., J. Jaramillo, 10 IV 1999, 1 ex., Trisd; **Tolima**, Prado, 321 m, 3°45'11"N/74°55'59"W, 26 XI 1989, 1 ex., M. Beltrán; **Tolima**, Saldaña, 310 m, 3°56'05"N/75°01'13"W, 2 IV 1997, 1 ex., A. Ariza & L. Ferrucho.

Distribution. Colombia; Costa Rica; Cuba; Dominican Republic; Haiti; Jamaica; Nicaragua; Panama; Puerto Rico; Venezuela.

Canistra osculatii Guérin, 1855

Risaralda, Pereira, 2137 m, 4°49'02"N/75°41'54"W, 27 XI 1996, 1 ex., R. Humberto.

Distribution. Brazil; Colombia; Ecuador; Peru.

Charidotella balteata (Champion, 1894)

Antioquia, San Antonio de Prado, 1955 m, 6°11'N/75°39'W, IX 1981, 2 ex., G. Morales.

Distribution. Panama. **New to Colombia.**

Charidotella carnulenta (Erichson, 1847)

Caqueta, San Vicente del Caguan, Vda. El Tigre, 480 m, 2°07'N/74°46'W, 25 III 2002, 1 ex., J. Méndez & E. García; **Meta**, Villavicencio, 467 m, 4°09'N/73°39'W, 24 V 1969, 1 ex., J.R. Alba.

Distribution. Argentina; Bolivia; Colombia; Peru; Venezuela.

Charidotella circumnotata (Boheman, 1862)

Antioquia, San Luis, 1050 m, 6°02'N/74°59'W, I 1986, VII 1983, 1 ex., G. Morales; **Huila**, Neiva, 442 m, 2°55'46"N/75°17'31"W, 13 IV 1967, 1 ex., H. Ramos;

Santander, Bucaramanga, 958 m, 7°07'17"N/73°07'33"W, 11 IV 1990, 1 ex., C. Sarmiento.

Distribution. Bolivia; Brazil; Costa Rica; Ecuador; French Guyana; Nicaragua; Panama; Peru. **New to Colombia.**

***Charidotella glaucovittata* (Erichson, 1847)**

Cundinamarca, Guayabetal, 1200 m, 4°13'N/73°48'W, 1 V 1969, 1 ex., L.M. Rico & C. Cujia; **Meta**, Puerto López, 181 m, 4°05'N/72°58'W, 4 X 1974, 1 ex., J. Britton; **Valle del Cauca**, Jamundi, 975 m, 3°15'N/76°32'W, 23 VI 1972, 1 ex., E. Leño.

Distribution. Bolivia; Ecuador; Paraguay; Peru. **New to Colombia.**

***Charidotella immaculata* (Olivier, 1790)**

Cundinamarca, Sasaima, 1225 m, 4°57'N/76°26'W, 5 III 1971, 1 ex., L. Morales; **Cundinamarca**, Tibacuy, Ins. Pol Cumaca, 1647 m, 4°21'N/74°27'W, 18 XI 1994, 1 ex., Reina; **Cundinamarca**, Villeta, 804 m, 5°00'52"N/74°28'23"W, 17 VI 1966, 1 ex., E. Aponte; **Huila**, Timaná, 1010 m, 1°58'N/75°56'W, 25 VI 1971, 1 ex., L. Morales; **Meta**, Cubarral, San Luis de Cubarral, Brisas del Ariari, 180 m, 3°47'N/73°52'W, 9 IV 2004, 1 ex., L. Ramirez & A. Vargas; **Tolima**, Melgar, 323 m, 4°12'24"N/74°38'44"W, 19 III 1969, 1 ex, C. Forero.

Distribution. Argentina; Bolivia; Brazil; Dominica; Colombia; Ecuador; French Guyana; Paraguay; Peru; Surinam; Trinidad and Tobago; Venezuela.

***Charidotella incorrupta* (Boheman, 1855)**

Meta, Villavicencio, 467 m, 4°09'N/73°39'W, 1 X 1975, 1 ex., C. Rodriguez; **Tolima**, Espinal, 322 m, 4°09'N/74°53'W, 27 IV 1969, 1 ex., E. Orjuela.

Distribution. Bolivia; Brazil; Colombia; Costa Rica; Ecuador; Panama; Peru; Venezuela.

***Charidotella liquida* (Erichson, 1847)**

Cundinamarca, Sasaima, 1225 m, 4°57'N/76°26'W, 8 III 1975, 1 ex., A. Alarcón; **Meta**, Cubarral, Finca Brisas del Ariari, 180 m, 3°47'N/73°52'W, 21 XI 2003, 1 ex., L. Pérez.

Distribution. Bolivia; Peru. **New to Colombia.**

***Charidotella moraguesi* Borowiec, 2007b**

Tolima, Carmen de Apicalá, Finca La Ponderosa, 328 m, 4°09'00"N/75°46'37"W, 23 X 1998, 1 ex., H. Parada.

Distribution. French Guyana. **New to Colombia.**

***Charidotella puella* (Boheman, 1855)**

Antioquia, Carepa, Granja Tulenapa, 28 m, 7°46'00"N/76°39'58"W, 14 IX 2001, 1 ex., G. Morales; **Antioquia**, Puerto Triunfo, Rio Claro, 115 m, 5°52'N/74°38'W, V 1985, 1 ex., A. Madrigal, VI 1985, 1 ex., R. Vélez; **Meta**, Acacias, 522 m, 4°00'N/73°46'W, 19 VIII 1976, 1 ex., S. Rodriguez; **Cundinamarca**, Tocaima, 400 m, 4°27'N/74°38'W, 2 XI 1973, 1 ex., O. Barbosa; **Meta**, Villavicencio, 467 m, 4°09'N/73°39'W, 1 X 1975, 1 ex., C. Rodriguez; **Tolima**, Armero, 352 m, 4°57'N/74°54'W, 14 IX 1980, 1 ex., E. Maldonado.

Distribution. Belize; Colombia; Costa Rica; Ecuador; French Guyana; Mexico; Honduras; Nicaragua; Panama; Peru; Venezuela.

***Charidotella seipunctata* (Fabricius, 1781)**

Antioquia, Concepción, 1862 m, 6°23'55"N/75°15'22"W, II 1997, 1 ex., F.J. Serna & J.G. Hurtado; **Antioquia**, San Luis, 1050 m, 6°02'50"N/74°59'50"W, IV 1995, 1 ex., Silva; **Cundinamarca**, Apulo, 421 m, 4°31'N/74°35'W, 8 VI 1984, 1 ex., Morales; **Cundinamarca**, Bogotá, 2620 m, 4°35'56"N/74°04'51"W, 30 V 1990, 1 ex., B. Diaz; **Cundinamarca**, Fusagasugá, 1746 m, 4°20'N/74°21'W, 4 III 1990, 1 ex., A. Pagos; **Cundinamarca**, Girardot, 150 m, 4°30'N/75°45'W, 7 XI 1970, 1 ex., A. Suárez, 24 XI 2001, 1 ex., D. Moreno; **Cundinamarca**, Guaduas, 1007 m, 5°04'N/74°35'W, 30 VI 1966, 1 ex., M. Pelaez, no date, 1 ex., O. Moro; **Cundinamarca**, Guayabetal, 4°13'40"N/73°48'59"W, 14 X 1970, 1 ex., H. Hernández; **Cundinamarca**, La Mesa, 1298 m, 4°38'05"N/74°27'57"W, 10 IX 1994, 1 ex., A. Pinilla; **Cundinamarca**, La Mesa, San Javier, 1298 m, 4°38'05"N/74°27'57"W, 1 VI 1997, 1 ex., A. Alessandri; **Cundinamarca**, La Mesa, Vda. San Joaquin, 670 m, 4°38'05"N/74°27'57"W, 17 IV 2002, 1 ex., J. Gómez; **Cundinamarca**, La Palma, 1462 m, 5°21'51"N/74°23'51"W, 28 IX 1973, 1 ex., A. Pinilla; **Cundinamarca**, Mantata, 1924 m, 5°00'42"N/73°32'41"W, 3 V 1997, 1 ex., X. Medina; **Cundinamarca**, Silvania, 1470 m, 4°24'21"N/74°23'24"W, 2 XI 1994, 2 ex., C. Ferro, 15 III 1997, 1 ex., C. Bojacá; **Cundinamarca**, Villeta, Vda. Topacio, 842 m, 5°00'N/74°28'W, 31 X 1970, 1 ex., L. Sánchez; **Cundinamarca**, Viotá, 567 m, 4°26'31"N/74°31'33"W, 6 VI 1989, 1 ex., F. Ramirez; **Huila**, Neiva, 442 m, 2°55'46"N/75°17'31"W, 25 V

1974, 1 ex., C. Reyes; **Meta**, Acacias, 522 m, 4°00'N/73°46'W, 1 V 1974, 1 ex., I. Oviedo, 28 III 1975, 1 ex., B. Correa; **Meta**, Guamal, 518 m, 3°51'N/73°45'W, 2 VIII 1968, 1 ex., S. Bobadillo, 21 V 1994, 1 ex., López & Rico; **Meta**, Puerto López, 450 m, 4°06'01"N/72°57'22"W, 27 V 2005, 1 ex., J. Castro, 26 V 2005, 1 ex., D. Rios; **Meta**, Villavicencio, 467 m, 4°09'N/73°39'W, 8 VI 1969, 1 ex., S. Martinez, 28 VI 1970, 1 ex., H. Osorio; **Santander**, Bucaramanga, 958 m, 7°07'17"N/73°07'33"W, 2 XI 1973, 1 ex., Castellano; **Santander**, La Belleza, 1900 m, 5°51'N/73°58'W, 28 III 1972, 1 ex., L. Angulo; **Santander**, Socorro, 1219 m, 6°25'N/73°14'W, 1 ex., L. Arenas & R. Lesmes; **Tolima**, El Guamo, 323 m, 4°02'05"N/74°58'25"W, 16 X 2001, 1 ex., A. Sarmiento; **Tolima**, Espinal, 322 m, 4°09'N/74°53'W, 19 V 2003, 1 ex., M. Capera & C. Jerez; **Tolima**, Honda, 229 m, 5°12'N/74°44'W, 3 IV 1974, 1 ex., E. Guevara; **Tolima**, Ibagué, 1285 m, 4°26'50"N/75°14'44"W, 30 I 1981, 1 ex., L. Lueñas; **Tolima**, Melgar, 323 m, 4°12'24"N/74°38'44"W, 1 X 1975, 1 ex., L. Méndez; **Tolima**, Purificación, 310 m, 3°51'N/74°56'W, 4 IV 1969, 1 ex., B. Vásquez; **Valle del Cauca**, Caicedonia, 1400 m, 4°19'25"N, 75°50'00"W, 16 X 2001, 1 ex., C. Prada.

Distribution. widespread from Canada to northern Argentina, include Brazil.

***Charidotella tuberculata* (Fabricius, 1775)**

Meta, Granada, 450 m, 3°32'N/73°43'W, 20 IX 1989, 1 ex., G. Villalba; **Tolima**, Falán, 998 m, 5°07'35"N/74°57'18"W, 10 IV 1990, 1 ex., Y. Beltrán.

Distribution. Colombia; Costa Rica; El Salvador; Guatemala; Honduras; Mexico; Nicaragua; Venezuela.

***Charidotella vinula* (Boheman, 1855)**

Cundinamarca, Sasaima, 1225 m, 4°57'59"N/76°26'15"W, 23 V 1967, 1 ex., E. Delgado; **Cundinamarca**, Viotá, El Triunfo, 567 m, 4°26'N/74°31'W, 10 III 1968, 1 ex., S. Sánchez; **Valle del Cauca**, La Unión, Fca. Grajales, 1250 m, 4°35'N 76°15'W, 14 X 2003, 1 ex., A. Molano.

Distribution. Argentina; Bolivia; Brazil; Colombia; Ecuador; French Guyana; Guyana; Mexico; Paraguay; Surinam; Venezuela.

***Charidotis bipartita* (Boheman, 1855)**

Santander, Puerto Wilches, 75 m, 7°20'52"N/73°54'25"W, 15 I 1993, 1 ex., G. Vargas.

Distribution. Brazil; French Guyana; Honduras; Panama; Venezuela. **New to Colombia.**

***Charidotis cincticula* (Boheman, 1855)**

Cundinamarca, Villeta, 842 m, 5°00'52"N/74°28'23"W, 28 V 1990, 1 ex., R. Suárez.

Distribution. Bolivia; Brazil; Ecuador; French Guyana; Peru. **New to Colombia.**

***Charidotis vitreata* (Perty, 1830)**

Antioquia, Amalfi, Cañón del Porce, Calandria, 985 m, 6°55'N/75°04'W, 14 I 1998, 1 ex., J. Hurtado.

Distribution. Argentina; Brazil; Colombia; Guatemala; Mexico; Nicaragua; Panama; Peru.

***Chelymorpha cavata* Boheman, 1854**

Cundinamarca, Guayabetal, 1200 m, 4°13'N/73°48'W, 1 V 1969, 1 ex., L.M. Rico & C. Cujia.

Distribution. Colombia; Venezuela.

***Chelymorpha marginata* (Linnaeus, 1758)**

Cesar, Valledupar, 182 m, 9°29'N/73°15'W, 5 IV 1972, 1 ex., J. Avellano; **Cundinamarca**, Guayabetal, 1200 m, 4°13'N/73°48'W, 1 V 1969, 1 ex., C. Cujia, 11 V 1972, 1 ex., E. Daza; **Cundinamarca**, Medina, 431 m, 4°38'54"N/73°19'37"W, 14 X 1989, 1 ex., C. Franco; **Cundinamarca**, Tocaima, 400 m, 4°27'N/74°38'W, 17 V 1969, 1 ex., A. Guzmán.

Distribution. Bolivia; Brazil; Colombia; Ecuador; French Guyana; Paraguay; Surinam; Venezuela.

***Chelymorpha testaceomarginata* Boheman, 1854**

Boyacá, Sogamoso, 2569 m, 5°42'58"N/72°55'38"W, 8 VI 1967, 1 ex., Plazas; **Cundinamarca**, Bogotá, 2620 m, 4°35'56"N/74°04'51"W, 3 IV 1969, 1 ex., Plazas; **Cundinamarca**, Girardot, 281 m, 4°18'18"N/74°48'08"W, 6 XI 1989, 1 ex., E. González; **Cundinamarca**, Guaduas, 1007 m, 5°04'N/74°35'W, 27 IX 1975, 1 ex., D. Moreno; **Cundinamarca**, La Mesa, San Javier, 1298 m, 4°38'05"N/74°27'57"W, 1 ex., Barbosa & Garcés, 1110 m, 4°38'N/74°27'W, 2 IV 1972, 1 ex., G. Arguelles; **Cundinamarca**, Pacho, 1798 m, 5°07'57"N/74°09'42"W, 20 V 1992, 1 ex., R. Chizaba, 8 IV 1995, 1 ex., P. Carlos; **Cundinamarca**, Villeta, 842 m, 5°00'N/74°28'W, 12 XI 1981, 1 ex., C. Orjuela; **Huila**, Neiva, 442 m, 2°55'N/75°17'W, 10 VII 1972, 1 ex., F. Gutierrez;

Meta, Villavicencio, 467 m, 4°09'N/73°39'W, 6 X 1975, 1 ex., J. Gómez; **Norte de Santander**, Cúcuta, 320 m, 7°53'N/72°30'W, 14 IX 1974, 1 ex., L. Ojeda; **Tolima**, Mariquita, 328 m, 5°12'N/74°55'W, 22 VI 1976, 1 ex., J. Nieto; **Valle del Cauca**, Buga, 969 m, 3°54'06"N/76°18'14"W, 20 IV 1994, 1 ex., Lizarrazo & Barriga.

Distribution. Colombia; Costa Rica; Dominican Rep.; Panama; Venezuela, N Brazil. Probably many records of *Chelymormpha cribraria* (F.) from northwestern part of South America belongs to *Ch. testaceomarginata* Boh.

Chersinellina heteropunctata (Boheman, 1854)

Córdoba, Monteria, Tres Palmas, 18 m, 8°29'N/75°56'W, VI 1973, 1 ex., R. Vélez; **Cundinamarca**, Fusagasugá, 1746 m, 4°20'49"N/74°21'53"W, X 1994, 1 ex., M. Ahumada.

Distribution. Colombia; Panama.

Cistudinella foveolata Champion, 1894

Guaviare, San Jose del Guaviaré, 240 m, 2°33'N/72°38'W, III 1996, 1 ex., C. Forero.

Distribution. Colombia; Costa Rica; Ecuador; Panama.

Coptocyclus n. sp. Sekerka & Windsor, in prep.

Coptocyclus dorsoplagiata Champion, 1894 (ex parte).

Coptocyclus rufonotata sensu Spaeth, 1936c: 255; Windsor et al. 1992: 390; Borowiec 1996: 225 (as *Psalidonota rufonotata*) all misinterpretations.

Antioquia, Jericó, 1967 m, 5°47'39"N/75°47'23"W, 1996, 1 ex., C. Tamayo.

Distribution. Colombia; Costa Rica; Panama; Venezuela.

Note: Spaeth (1936c) misinterpreted *Coptocyclus rufonotata* Champion, 1893 and recent records of this taxon (Windsor et al. 1992: 390; Borowiec 1996: 225) concern an undescribed species. Its formal description is now under preparation by Sekerka and Windsor in their review of the Panamanian tortoise beetles.

Cteisella divalis Spaeth, 1926b

Cundinamarca, Girardot, 150 m, 4°30'N/75°45'W, 19 III 1969, 1 ex., Junca; **Tolima**, Honda, 229 m, 5°12'25"N/74°44'28"W, 8 V 1966, 1 ex., E. Guzmán, 1 ex., O. Pedraza.

Distribution. Colombia; Panama; Venezuela.

***Cyrtonota bergeali* Borowiec & Sassi, 1999**

Valle del Cauca, Calima, C. Alegre, 1414 m, 3°55'N, 76°40'W, IV 1990, 2 exx., L.C. Pardo-Locamo.

Distribution. known only from Valle del Cauca in Colombia.

***Cyrtonota dissecta* (Boheman, 1850)**

Cundinamarca, San Antonio del Tequendama, 1521 m, 4°37'04"N/74°21'15"W, 27 IV 1990, 1 ex., M. Fuentes; **Cundinamarca**, Viotá, 567 m, 4°26'31"N/74°31'33"W, 10 V 1966, 1 ex., P. Mendoza; **Risaralda**, Ucumari, vereda El Bosque, V 2000, 1 ex., J. Sáenz.

Distribution. Colombia; Peru.

***Cyrtonota goryi* (Boheman, 1850)**

Meta, Villavicencio, 467 m, 4°09'N/73°39"W, 24 V 1969, 1 ex., J.R. Alba.

Distribution. known only from Colombia.

***Cyrtonota moderata* (Spaeth, 1913)**

Caldas, Guática, 1820 m, IX 1994, 1 ex., A. Madrigal; **Quindío**, Armenia, 1483 m, 4°31'N/75°42'W, I 2000, 1 ex., A. Madrigal.

Distribution. known only from Colombia.

***Cyrtonota steinheili* (Wagener, 1877)**

Cundinamarca, La Mesa, 1298 m, 4°38'05"N/74°27'57"W, 5 IV 1994, 1 ex., H. Rodríguez.

Distribution. Colombia; Peru.

***Cyrtonota textilis* (Boheman, 1850)**

Cundinamarca, Apulo, 421 m, 4°31'18"N/74°35'58"W, 16 IX 1995, 1 ex., Fredy; **Cundinamarca**, Bojacá, Vda. Bojacá, El Chilcal, 1950 m, 4°44'N/74°20'W, 5 V 2001, A. Osorio & C. Zuluaga; **Cundinamarca**, La Mesa, Laguna Pedro Palo, 1298 m, 4°38'05"N, 75°11'7"W, 20 III 1993, 1 ex., P. Osorio, 2031 m, 4°41'07"N/74°23'50"W, 16 IV 1994, 1 ex., D. Moreno, 1298 m, 2 XI 1996, 1 ex.,

A. Romero, 2031 m, IX 1998, 1 ex., J. Muñoz; **Cundinamarca**, La Mesa, Laguna Pedro Palo, Quebrada Patio Bonito, 1298 m, 4°38'05"N/74°27'57"W, 1 ex., J. Martínez & D. Vegas; **Cundinamarca**, Pandi, 1024 m, 4°11'40"N/74°29'50"W, 12 X 1995, 1 ex., T. Corredor; **Cundinamarca**, San Antonio del Tequendama, 1500 m, 4°37'N/74°21'W, 1 V 2001, 1 ex., C. Martínez, J. Muñoz & J. Abello; **Cundinamarca**, San Bernardo, 1600 m, 4°11'10"N/74°24'31"W, 19 IX 1989, 1 ex., M. Pava; **Cundinamarca**, Soacha, 2568 m, 4°35'03"N/74°13'23"W, 2 IX 1989, 1 ex., A. Martínez; **Cundinamarca**, Tena, 1384 m, 4°39'33"N/74°23'28"W, 17 XI 1993, 1 ex., H. Rondón, 30 III 1994, 2 ex., A. Tovar; **Cundinamarca**, Villeta, Vda. Topacio, 842 m, 5°00'N/74°28'W, 6 IV 2001, 1 ex., A. Afanador & C. Berdugo; Guainia, Puerto Inirida, 100 m, 3°49'N/67°52'W, 16 V 1992, 1 ex., S. Bernal; **Huila**, Neiva, 442 m, 2°55'46"N/75°17'31"W, 1 ex., H. Trujillo; **Meta**, Granada, 450 m, 3°32'N/73°43'W, 1 V 1994, 1 ex., N. Pinzón; **Meta**, Villavicencio, 467 m, 4°9'N/73°39'W, 3 IV 1994, 1 ex., C. Pérez; **Tolima**, Cajamarca, El Tigre, 1814 m, 4°26'N/75°25'W, 27 V 2002, 1 ex., J. Martínez; **Tolima**, Guamo, 323 m, 4°02'05"N/74°58'25"W, 20 V 1995, 1 ex., T. Rene; **Tolima**, Ibagué, 1285 m, 4°26'50"N/75°14'44"W, 18 IX 1998, 1 ex., A. Rubio; **Valle del Cauca**, Sevilla, 1612 m, 4°16'06"N/75°57'13"W, 3 I 1990, 1 ex., M. Caro

Distribution. known only from Colombia.

Delocrania cossyphoides Guérin, 1844

Magdalena, San Sebastián de Buenavista, 25 m, 9°23'N/74°11'W, 27 II 1994, 4 exx. on Palma ornamental, A. Madrigal; **Santander**, Puerto Wilches, 75 m, 7°20'52"N/73°54'25"W, 2 VIII 2004, 1 ex., D. Ávila.

Distribution. Brazil; Trinidad; Venezuela. **New to Colombia.**

Deloyala fuliginosa (Olivier, 1790)

Córdoba, Montería, 19 m, 8°45'N/75°52'W, IX 1972, 1 ex., R. Vélez.

Distribution. Belize; Brazil; Colombia; Costa Rica; Cuba; Dominican Republic; El Salvador; Guatemala; Martinique; Mexico; USA: Texas; Nicaragua; Panama; Venezuela.

Deloyala insubida (Boheman, 1855)

Antioquia, Amalfí, Cañón del Porce, 1050 m, 6°55'N/75°04'W, 1997, 1 ex., J. Hurtado; **Cundinamarca**, Arbeláez, 1417 m, 4°16'N/74°24'W, 1 XI 1973, 1 ex., A. González; **Cundinamarca**, La Mesa, 1298 m, 4°38'05"N/74°27'57"W, 8 IV 1970, 1 ex., L. Moreno, 1 IV 1997, 1 ex., J. Camargo; **Cundinamarca**, La Mesa, via a Mesitas, 1298 m, 4°38'05"N/74°27'57"W, 19 VI 1998, 1 ex., C. Navas; **Meta**, Villavi-

cencio, Puerto Lopez, 450 m, 3°08'N/73°45'W, 26 V 2005, 1 ex., D. Rios; **Tolima**, Armero, 352 m, 4°57'N/74°54'W, 10 XII 1965, 1 ex., Pérez; **Tolima**, Ibagué, 1285 m, 4°26'50"N/75°14'44"W, 25 IV 1978, 1 ex., G. Vargas; **Tolima**, Melgar, 323 m, 4°12'24"N/74°38'44"W, 31 III 1972, 1 ex, M. Acosta.

Distribution. Colombia; Costa Rica; Ecuador; Panama; Venezuela.

Discomorpha amazona (Spaeth, 1940)

Meta, Cumaral, 480 m, 4°17'N/73°33'W, 29 IX 1973, 1 ex., A. Vargas; **Meta**, Villavicencio, 469 m, 4°09'N/73°39'W, 14 X 1994, 1 ex., F. Montes; **Santander**, Oiba, Vda. Pedregal, 1452 m, 6°15'N/73°15'W, 4 VI 2003, 1 ex., J. Cárdenas.

Distribution. Colombia; Peru.

Discomorpha batesi (Boheman, 1856)

Antioquia, Ituango, 1675 m, I 1989, 1 ex., D. Calle.

Distribution. Brazil; Colombia; Peru.

Discomorpha biplagiata (Guérin-Méneville, 1844)

Casanare, Mani, 200 m, 4°49'N/72°17'W, 22 III 1967, 2 exx., Plazas; **Casanare**, Yopal, 350 m, 5°21'N/72°24'W, 5 V 1967, 1 ex., H. Lizarazo; **Cundinamarca**, Girardot, 281 m, 4°18'18"N/74°48'08"W, 31 VIII 1924, 1 ex., J. Rincón; **Cundinamarca**, Guayabetal, 1200 m, 4°13'N/73°48'W, 4 V 1969, 1 ex., H. Muñoz & O. Millán; **Cundinamarca**, Villeta, 842 m, 5°00'N/74°28'W, 4 VII 1972, 1 ex., A. Canunes; **Huila**, Neiva, 442 m, 2°55'46"N/75°17'31"W, 20 X 1974, 1 ex., J. Ruiz; **Meta**, Cumaral, 480 m, 4°17'N/73°33'W, 5 XII 1988, 1 ex.; **Meta**, Guamal, 518 m, 3°51'N/73°45'W, 19 X 1994, 1 ex., Pinilla; **Meta**, La Macarena, 3°11'16"N/734°59'20"W, 29 III 1997, 1 ex., C. Santana; **Meta**, San Juan de Arama, 450 m, 3°22'N/73°52'W, VIII 1969, 1 ex.; **Meta**, San Martin, 419 m, 3°42'N/73°42'W, 20 VIII 1974, 1 ex., F. Garzón, 30 III 1994, 1 ex., A. Avella; **Meta**, Villavicencio, 467 m, 4°09'N/73°39'W, VI 1967, 2 exx., Cardona, 17 VI 1967, 1 ex., J. Carrillo, 10 V 1969, 1 ex., J. López, 20 VI 1969, 1 ex., M. Barreto, 1 III 1972, 2 exx., I. Garzón, 1 III 1972, 1 ex., G. Guzmán, 20 VII 1974, 1 ex., R. Granados, 16 XII 1974, 1 ex., L. Torres, 2 XI 1981, 1 ex., C. Orjuela & E. Mejia; **Tolima**, Espinal, 322 m, 4°09'N/74°53'W, 11 VI 1975, 1 ex., D. Martinez; **Tolima**, Fresno, 1473 m, 5°09'16"N/75°02'23"W, 19 II 1967, 1 ex., A. Moreno; **Tolima**, Honda, 224 m, 5°12'25"N/74°44'28"W, 5 I 1975, 1 ex., 4 I 1995, 1 ex., R. Granados; **Valle del Cauca**, Cali, 987 m, 3°26'N/76°31'W, 11 XI 1974, 1 ex., A. Contreras.

Distribution. Brazil; Colombia; Ecuador; Peru; Venezuela.

***Discomorpha spectanda* (Boheman, 1862)**

Magdalena, Mompox, 9°21'44"N/79°59'8"W, IX 1982, 1 ex. on *Tabebuia rosea*, A. Madrigal.

Note. The species is not associated with *Tabebuia rosea* and was most likely just sitting on the plant as *Discomorpha* is associated with Boraginaceae, dominantly the genus *Cordia* (L. Sekerka pers. comm.).

Distribution. Known only from Colombia.

***Discomorpha panamensis* (Spaeth, 1919b)**

Antioquia, San Luis, 1050 m, 6°02'50"N/74°59'59"W, 25 IX 1989, 1 ex., C. Rincón.

Distribution. Panama. **New to Colombia.**

***Dorynota kiesenwetteri* (Boheman, 1854)**

Meta, Villavicencio, 467 m, 4°09'N/73°39'W, 1 XI 1974, 1 ex., A. Yañez.

Distribution. Bolivia; Brazil; Colombia; Peru.

***Dorynota nodosa* (Boheman, 1854)**

Sucre, El Piña, 237 m, 9°27'N/75°12'W, 10 VII 1998, 1 ex., E. Vergara.

Distribution. Colombia; Panama; Venezuela.

***Dorynota rufomarginata* (Wagner, 1881)**

Meta, Villavicencio, 467 m, 4°09'N/73°39'W, 11 VII 1974, 1 ex., J. Pabón.

Distribution. Brazil. **New to Colombia.**

***Echoma anaglyptoides* Borowiec, 1998b**

Cundinamarca, Bituima, 1412 m, 4°52'31"N/74°32'33"W, 16 V 1989, 1 ex., M. Buitrago, 2 V 1992, 1 ex., O. Bilvaio; **Cundinamarca**, Nimaima, Inspección de Policía de Tobia, 1185 m, 5°07'44"N/74°23'20"W, 10 I 1990, 1 ex., J. Garcia; **Cundinamarca**, Pacho, 1798 m, 5°07'N/74°09'W, 4 XI 1989, 1 ex, en Melastomataceae, C. Berrio; **Tolima**, Chaparral, La Granja, Barrio Baltrán, 850 m, 3°43'N/75°29'W, 5 IV 2002, 2 exx., M. Segura; **Tolima**, Espinal, 322 m, 4°09'10"N/74°53'19"W, 3 VI 1989, 1 ex., J. Rodriguez.

Distribution. Brazil; Colombia; French Guyana.

***Echoma clypeata* (Panzer, 1798)**

Meta, Villavicencio, 467 m, 4°09'N/73°39'W, 27 IX 1974, 1 ex., S. Vega.

Distribution. Bolivia; Brazil; Colombia; Ecuador; French Guyana; Guyana; Paraguay; Peru; Trinidad; Venezuela.

***Eugenysa columbiana* (Boheman, 1850)**

Boyacá, Otanche, 1050 m, 5°49'35"N/74°11'20"W, V 1994, 1 ex., A. Ortega; **Caldas**, Confines, Cariaño, 500 m, II 2002, 1 ex., E.E. Martinez; **W Cundinamarca**, Viani, 1498 m, 4°52'36"N/74°33'57"W, 24 IX 1985, 1 ex., Moro.

Distribution. Colombia; Costa Rica; Panama.

***Eugenysa martae* Borowiec, 1987**

Valle del Cauca, Calima, R. [= Río] Chancos, X 1990, 1 ex., L.C. Pardo-Locamo.

Distribution. known only from Colombia.

***Eugenysa unicolor* Borowiec & Dąbrowska, 1997**

Cesar, Aguachica, 162 m, 8°18'42"N/73°27'03"W, 10 VI 1972, 1 ex., J. Jiménez.

Distribution. Ecuador; Peru; **New to Colombia.**

***Eurypedus nigrosignatus* (Boheman, 1854)**

Atlántico, Barranquilla, 68 m, 11°00'N/74°48'W, 7 VII 1967, 1 ex., Laverde; **Caldas**, Victoria, 700 m, 5°19'N/74°54'W, 2 IX 1974, 1 ex., M. Calderón; **Casanare**, Yopal, La Nieta, Maracaito, 350 m, 5°21'N/72°24'W, 16 IX 2003, 1 ex., J. López; **Casanare**, Yopal, Via La Chaparrera, 350 m, 5°21'N/72°24'W, 25 VIII 1997, 1 ex., H. Alvarez; **Cundinamarca**, Apulo, 421 m, 4°31'N/74°35'W, 5 X 1969, 1 ex., C. Pinzón, 24 IV 1993, 1 ex., I. Guarinmelgar; **Cundinamarca**, Bogotá, 2600 m, 4°35'56"N/74°04'51"W, 21 X 1966, 1 ex., J. Ortiz; **Cundinamarca**, Bogotá, Parque Simón Bolívar, 2620 m, 4°35'56"N/74°04'51"W, 20 XI 2001, 1 ex., W. Cañón; **Cundinamarca**, Choachi, 1927 m, 4°31'53"N/73°55'36"W, 20 III 2001, 1 ex., J. Valderama; **Cundinamarca**, Girardot, 281 m, 4°18'18"N/74°48'08"W, 15 V 1975, 1 ex., B. Guzman, 150 m, 4°30'N/75°45'W, 5 XI 1994, 1 ex., M. Beltrán, 24 XI 2001, 1 ex., D. Moreno; **Cundinamarca**, Guayabetal de Siquima, 1630 m, 4°52'N/74°28'W, 24 V 1964, 1 ex., N. Correa, 26 X 1969, 1 ex., C. Pinzón; **Cundinamarca**, La Mesa, Vda. San Joaquin, 670 m, 4°38'05"N/74°27'57"W, 17

IV 2002, 1 ex., J. Gómez, 17 IV 2002, 1 ex., A. Bejarano, 17 IV 2002, 1 ex., J. Cárdenas, 1700 m, 17 IV 2002, 1 ex., H. Duque; **Cundinamarca**, La Mesa, Via Tocaima, 1298 m, 4°38'N/74°27'W, 3 IV 1993, 1 ex., C. Omar; **Cundinamarca**, Nariño, 400 m, 4°24'N/74°50'W, 27 III 1975, 1 ex., A. Mendoza; **Cundinamarca**, Pacho, 1798 m, 4°18'18"N/74°48'08"W, 2 V 1998, 1 ex., Amorochó & Gómez; **Cundinamarca**, Pacho, Los Algarrobos, 1798 m, 5°07'N/74°09'W, 21 X 1997, 1 ex., J. Gross; **Cundinamarca**, Tocaima, 400 m, 4°27'40"N/74°38'10"W, 15 I 1961, 1 ex., A. Enciso, 24 IV 1969, 3 ex., L. Rico & C. Cujía, 28 III 1984, 2 ex., L. Sarmiento; **Cundinamarca**, Útica, 497 m, 5°11'45"N/74°29'03"W, 2 IV 1966, 3 ex., 3 IV 1966, 2 ex., J. Ortiz; **Cundinamarca**, Villeta, 842 m, 5°00'N/74°28'W, 17 VII 1966, 1 ex., E. Aponte, 18 X 1969, 1 ex., C. Pinzón; **Huila**, El Hobo, 276 m, 2°35'17"N/75°27'13"W, 11 V 1998, 1 ex., Amorochó & Gómez; **Huila**, Neiva, 442 m, 2°55'N/75°17'W, 13 IV 1964, 1 ex., F. Ramos, 25 V 1974, 5 ex., C. Reyes; **Meta**, Acacias, 522 m, 4°00'N/73°46'W, 13 X 1973, 1 ex., B. Torres; **Norte de Santander**, Cúcuta, 320 m, 7°53'N/72°30'W, 3 IV 1969, 1 ex., 3 IV 1969, 1 ex., 4 IV 1969, 1 ex., R. Lemus, 16 VII 1974, 1 ex., R. Granados, 20 VII 1974, 2 ex., J. Gómez, 9 X 1974, 1 ex., C. Melo; **Tolima**, Espinal, 322 m, 4°09'10"N/74°53'19"W, 19 V 1966, 1 ex., H. Ayala, 1 III 1967, 1 ex., Bernal; **Tolima**, Espinal, Ins. Pol. Chicoral, 322 m, 4°09'N/74°53'W, 23 XII 1969, 1 ex., J.D. Moreno; **Tolima**, Guamo, 200 m, 3°45'N/76°54'W, 8 XI 1996, 1 ex., K.R., 8 XII 2001, 1 ex., D. Moreno; **Tolima**, Honda, 229 m, 5°12'25"N/74°44'28"W, 8 V 1966, 1 ex., E. Guzmán, 1 ex., A. González; **Tolima**, Mariquita, 328 m, 5°12'10"N/74°55'49"W, 24 VII 1966, 1 ex., G. Pedraza, 22 IX 1993, 1 ex., P. Bolívar; **Tolima**, Melgar, 323 m, 4°12'N/74°38'W, 20 VII 1966, 1 ex., H. Santos, 1 V 1967, 1 ex., G. Torrado, 1 X 1994, 1 ex., W. Valera.

Distribution. Colombia; Guatemala; Nicaragua; Panama; Venezuela.

Helocassis crucipennis (Boheman, 1855)

Sucre, San Marcos, Santa Inés, 29 m, 8°40'N/75°08'W, 26 VI 2003, 1 ex., A. Díaz.

Distribution. Belize; Colombia; Costa Rica; Guatemala; Honduras; Mexico; Nicaragua; Panama; Venezuela.

Helocassis testudinaria (Boheman, 1855)

Antioquia, Santafé de Antioquia, 1567 m, 6°11'N/75°34'W, XII 1986, 3 ex., R. Vélez; **Cundinamarca**, Ricaurte, 287 m, 4°16'38"N/74°46'41"W, 29 III 1994, 1 ex., H. Gómez; **Cundinamarca**, Villeta, Vda. Guamalotal, 842 m, 5°00'N/74°28'W, 25 IX 2000, 1 ex., Urrea & Tamara.

Distribution. Belize; Colombia; Costa Rica; El Salvador; Guatemala; Honduras; Mexico; Panama; USA: Arizona, Florida; Venezuela.

***Hilarocassis bordoni* Borowiec, 2002a**

Cundinamarca, Girardot, 150 m, 4°30'N/75°45'W, 9 IV 1994, 1 ex., A. Silva; **Cundinamarca**, Guayabe tal, 1200 m, 4°13'N/73°48'W, 1 IV 1969, 1 ex., C. Acosta; **Cundinamarca**, La Mesa, 1298 m, 4°38'05"N/74°27'57"W, 15 IX 1996, 1 ex., C. Pinzón; **Cundinamarca**, Mesitas del Colegio, Fca. Las Brisas, 1100 m, 4°35'N/74°26'W, 9 III 2002, 1 ex., A. Bejarano.

Distribution. Venezuela. **New to Colombia.**

***Hybosa galbanata* Boheman, 1855**

Caldas, La Dorada, 178 m, 5°27'N/74°40'W, 10 V 1971, 1 ex., 15 X 1971, 1 ex., J. Zapata.

Distribution. known only from Colombia.

***Ichnocodia annulus* (Fabricius, 1781)**

Cundinamarca, Bogotá, El Paraiso, 2620 m, 4°35'56"N/74°04'51"W, 9 IX 1997, 1 ex., M. Alape; **Cundinamarca**, Cachipay, Insp. Pol. Anolaima, Vrda. San Cayetano, 5°16'22"N/74°34'22"W, 23 VII 1997, 1 ex., S. Olarte; **Cundinamarca**, Caqueza, 1746 m, 4°24'30"N/73°56'58"W, 12 IV 1997, 1 ex., A. Alessandri; **Cundinamarca**, La Mesa, Casco urbano, 1298 m, 4°38'05"N/74°27'57"W, 11 X 1997, 1 ex., E. Baron; **Cundinamarca**, La Mesa, San Javier, 1110 m, 4°38'N/74°27'W, 8 VI 1996, 1 ex., S. Dinas; **Cundinamarca**, La Mesa, Vrda. Guayabal, 1298 m, 4°38'05"N/74°27'57"W, 7 X 1997, 2 exx., M.A. & D.R.; **Cundinamarca**, Paime, 960 m, 5°22'16"N/74°09'18"W, 2 V 1992, 1 ex., Y. Castro; **Cundinamarca**, San Juan de Rio Seco, 1203 m, 4°50'54"N/74°37'35"W, 19 VIII 1998, 1 ex., J. Gutiérrez; **Cundinamarca**, Ubalá, Vrda. El Puerto, 1962 m, 4°44'48"N/73°32'18"W, 20 I 1998, 2 exx., M. Garcia; **Cundinamarca**, Villeta, Ecopetrol, 842 m, 5°00'52"N/74°28'23"W, 31 VIII 1997, 1 ex., R. Paredes; **Meta**, Cubarral, San Luis de Cubarral, Brisas del Ariari, 180 m, 3°47'N/73°52'W, 6 IV 2004, 1 ex., L. Ramirez & A. Vargas; **Meta**, La Macarena, 3°11'16"N/73°59'20"W, 26 III 1997, 1 ex., E. Bastidas; **Norte de Santander**, El Zulia, Rio Zulia, 220 m, 7°56'04"N/72°16'37"W, 2 XII 1998, 1 ex., F. Camacho; **Santander**, El Carmen de Chucuri, Vda. Dos Bocas, Fca. Playa Grande, 550 m, 6°46.514'N/73°38.408'W, XI 2003, 7 exx., L. Otero; **Santander**, La Belleza, Vrda. Los Naranjos, 1900 m, 5°51'57"N/73°58'02"W, 21 III 1997, 1 ex., H. Marin; **Valle del Cauca**, Buga, 969 m, 3°54'06"N/76°18'14"W, 14 X 2003, 1 ex., D. Quintana.

Distribution. Argentina; Belize; Bolivia; Brazil; Colombia; Costa Rica; Ecuador; El Salvador; French Guyana; Guatemala; Honduras; Mexico; Nicaragua; Panama; Paraguay; Trinidad; Venezuela.

***Microctenochira aspersa* (Champion, 1894)**

Antioquia, Cocorná, 6°3'25"N 75°11'7"W, 1286 m, VI 1977, 1 ex., R. Vélez; **Antioquia**, Concepción, 1862 m, 6°23'55"N/75°15'22"W, II 1997, 4 exx., F.J. Serna & J.G. Hurtado; **Cundinamarca**, Girardot, 150 m, 4°30'N/75°45'W, 13 VI 1967, 1 ex., Chavarriaga; **Cundinamarca**, Guayabetal, 1200 m, 4°13'N/73°48'W, 1 V 1969, 1 ex., L.M. Rico & C. Cujia; **Cundinamarca**, Sasaima, 1225 m, 4°57'59"N/76°26'15"W, 1 V 1970, 1 ex., E. Morales, VI, 1 ex., Jiménez; **Cundinamarca**, Viotá, 567 m, 4°26'31"N/74°31'33"W, 1 V 1996, 1 ex., L. Sánchez; **Magdalena**, Sevilla, VIII 1942, 2 exx., F.L. Gallego; **Meta**, Cubarral, San Luis de Cubarral, Brisas del Ariari, 180 m, 3°47'N/73°52'W, 6 IV 2004, 1 ex., L. Ramirez & A. Vargas; **Meta**, Villavicencio, 467 m, 4°09'N/73°39'W, 28 IV 1989, 1 ex., J. Rodriguez; **Santander**, Lebrija, 1015 m, 7°06'59"N 73°13'13"W, 12 V 1977, 1 ex., L. Rivera.

Distribution. Colombia; Costa Rica; Guatemala; Mexico; Panama.

***Microctenochira cumulata* (Boheman, 1855)**

Antioquia, San Andrés, 1530 m, VII 1952, 1 ex., F. Gallego.

Distribution. Colombia; Costa Rica; Ecuador; Guatemala; Mexico; Nicaragua; Panama; Venezuela.

***Microctenochira fairmairei* (Boheman, 1855)**

Antioquia, Amalfi, Cañón del Porce, Fosforito, 945 m, 6°45'37"N/75°06'28"W, 10 VI 1997, 2 exx., J. Hurtado; **Antioquia**, Amalfi, Cañón del Porce, Santa Lucía, 1050 m, 6°46'34"N/75°06'18"W, 31 VII 1997, 1 ex., J. Hurtado; **Antioquia**, San Roque, Vda. La Mora, Alto El Cuatro, 1800 m, 6°29'45"N/75°01'54"W, X 2008, 1 ex., H. Paredes.

Distribution. Bolivia; Colombia; Ecuador; Panama; Peru.

***Microctenochira flavonotata* (Boheman, 1855)**

Cundinamarca, La Mesa, 1298 m, 4°38'05"N/74°27'57"W, 11 VI 1989, 1 ex., A. Boada.

Distribution. Colombia; Costa Rica; Honduras; Nicaragua; Panama; Surinam; Trinidad; Venezuela.

***Microctenochira fraterna* (Boheman, 1855)**

Antioquia, Amalfi, Cañón del Porce, 6°55'N/75°04'W, 1050 m, 1997, 1 ex., J. Hurtado; **Antioquia**, La Estrella, 1764 m, 6°09'N/75°39'W, VI 1963, 1 ex., F.L. Gallego;

Antioquia, Santafé de **Antioquia**, 550 m, 6°33'N/75°49'W, III 1998, 1 ex., J.E. Jaramillo; **Cundinamarca**, San Cayetano, 2208 m, 5°18'N/74°04'W, 3 X 1970, 2 exx., A. Tobón; **Cundinamarca**, Tena, 1384 m, 4°39'33"N/74°23'28"W, 8 XII 1995, 1 ex., Porras; **Cundinamarca**, Viotá, 567 m, 4°26'31"N/74°31'33"W, 9 IV 1999, 1 ex., V. Contreras.

Distribution. Colombia; Costa Rica; Ecuador; Nicaragua; Panama; Trinidad and Tobago; Venezuela.

***Microctenochira jousselini* (Boheman, 1855)**

Boyacá, Maripi, Vrda. Santa Rosa, 800 m, 5°33'08"N/74°01'00"W, 12 IX 1999, 1 ex., C. Cortés.

Distribution. Colombia; Trinidad.

***Microctenochira lindigi* (Kirsch, 1865)**

Antioquia, La Unión, 2479 m, 5°58'N/75°21'W, 18 III 1998, 1 ex., J.E. Jaramillo; **Cundinamarca**, Medina, 431 m, 4°38'54"N/73°19'37"W, 16 X 1999, 1 ex., M. Acosta.

Distribution. Colombia; Bolivia; Ecuador; Venezuela.

***Microctenochira peltata* (Boheman, 1855)**

Cundinamarca, Sasaima, 1225 m, 4°57'59"N/76°26'15"W, 10 VI 1972, 1 ex., R. Arenas.

Distribution. Bolivia; Brazil; Ecuador; Peru. **New to Colombia.**

***Microctenochira quadrata* (DeGeer, 1775)**

Antioquia, Anori, 1574 m, 7°04'N/75°09'W, 5 IV 1985, 1 ex., R.R.D; **Cundinamarca**, Guayabetal, 1200 m, 4°13'N/73°48'W, 15 III 1969, 1 ex., A. Avila; **Cundinamarca**, Villeta, 842 m, 5°00'52"N/74°28'23"W, 26 V 1979, 1 ex., O. Garzón; **Meta**, Granada, 450 m, 3°32'N/73°43'W, 17 VII 1979, 1 ex., Gutierrez.

Distribution. Brazil; Colombia; French Guyana; Guyana; Panama; Paraguay; Surinam; Trinidad; Venezuela.

***Microctenochira semilobata* (Wagner, 1877)**

Antioquia, La Pintada, 678 m, 5°44'N/75°35'W, X 1971, 1 ex., R. Vélez.

Distribution. Brazil; Colombia.

***Microctenochira semilunaris* (Boheman, 1862)**

Boyacá, San Luis de Gaceno, 630 m, 4°49'21"N/73°10'13"W, 17V 1972, 1 ex., S. Cubides; **Cundinamarca**, Arbelaez, 1417 m, 4°16'37"N/74°24'35"W, 13 VIII 1994, 1 ex., N. Rocio; **Cundinamarca**, Medina, Finca Mi Negro, 431 m, 4°38'54"N/73°19'37"W, 16 X 1999, 1 ex., M. Acosta; **Cundinamarca**, Guayabetal, 1200 m, 4°13'40"N/73°48'59"W, 12 III 1970, 1 ex., M. Garcia; **Cundinamarca**, Guayabetal de Siquima, 1630 m, 4°52'N/74°28'W, 15 VIII 1968, 1 ex., E. Gil; **Cundinamarca**, Sasaima, 1225 m, 4°57'59"N/76°26'15W, 26 V 1967, 1 ex., E. Delgado; **Cundinamarca**, Silvania, 1470 m, 4°24'21"N/74°23'24"W, 7 IV 1978, 1 ex., A. Sánchez; **Cundinamarca**, Soacha, 2568 m, 4°35'N/74°13'W, 26 IV 1975, 1 ex., R. Herrera; **Cundinamarca**, Villeta, 842 m, 5°00'N/74°28'W, 1 X 1970, 1 ex., G. Garcia; **Meta**, Villavicencio, 467 m, 4°09'N/73°39'W, IV 1969, 1 ex., Preciado, 19 IV 1969, 1 ex., L. Castiblanco.

Distribution. Bolivia; Brazil; Colombia; Ecuador; French Guyana; Peru.

***Microctenochira sepulchlaris* (Boheman, 1855)**

Antioquia, Caldas, 1768 m, 6°05'N/75°38'W, XI 1973, 1 ex., A. Madrigal; **Antioquia**, Concepción, 1862 m, 6°23'55"N/75°15'22"W, II 1997, 1 ex., F.J. Serna & J.G. Hurtado.

Distribution. Colombia.

***Microctenochira sertata* (Erichson, 1847)**

Antioquia, Chigorodó, 34 m, 7°40'13"N/76°41'00"W, VIII 1975, 1 ex., D. Gonzalez; **Antioquia**, Concepción, 1862 m, 6°23'55"N/75°15'22"W, II 1997, 1 ex., F.J. Serna & J.G. Hurtado; **Bolivar**, Monpós, **Córdoba**, 33 m, 9°14'00"N/74°26'00"W, XII 1994, 1 ex., J.A. Quiróz; **Córdoba**, Tierra alta, P.N.N. Nudo Paramillo, Cerro Murrucucu, 287 m, 7°59'24.27"N/76°07'44.29"W, IX-X 2004, 1 ex. J.E. Arango; **Cundinamarca**, Guayabetal, 1200 m, 4°13'40"N/73°48'59"W, 30 III 1972, 1 ex., R. Gómez; **Cundinamarca**, Sasaima, 1225 m, 4°57'59"N/76°26'15"W, IV 1977, 1 ex., Jaramillo; **Cundinamarca**, Villeta, 842 m, 5°00'52"N/74°28'23"W, 3 VI 1972, 1 ex., L. Barbosa; **Cundinamarca**, Viotá, 567 m, 4°26'31"N/74°31'33"W, 1 V 1996, 1 ex., L. Sánchez; **Meta**, Acacias, 522 m, 4°00'N/73°46'W, 1 V 1974, 1 ex., I. Oviédo.

Distribution. Bolivia; Brazil; Colombia; Ecuador; French Guyana; Peru; Surinam; Venezuela.

***Omaspides bistrata* Boheman, 1862**

Valle del Cauca, B. Dagua-Esacalarete, VI 1990, 1 ex., L.C. Pardo-Locomo.

Distribution. Colombia; Costa Rica; Panama; Venezuela.

***Omaspides nitidicollis* Spaeth, 1937a**

Caldas, La Dorada, 178 m, 5°27'24"N/74°40'02"W, V 1994, 1 ex., M. Garcia

Distribution. Colombia.

***Omaspides specularis* (Erichson, 1847)**

Meta, San Martin, 419 m, 3°42'N/73°42'W, 29 IV 1989, 1 ex., C. Rincón.

Distribution. Brazil; Colombia; Ecuador; Peru.

***Parachirida semiannulata* (Boheman, 1855)**

Cundinamarca, Villeta, 842 m, 5°00'52"N/74°28'23"W, 28 II 1980, 1 ex., Cifuentes.

Distribution. Brazil; Colombia; Peru.

***Parachirida subirrorata* (Boheman, 1855)**

Córdoba, Montería, Tres Palmas, 18 m, 8°29'N/75°56'W, VII 1976, 1 ex., A. Madrigal; **Meta**, Cumaral, 480 m, 4°17'N/73°33'W, 16 IV 1989, 1 ex., C. Caballero; **Meta**, Villavicencio, 400 m, 4°09'N/73°39'W, 8 XI 2002, 1 ex., G. González; **Meta**, Villavicencio, Jardín Botánico, 400 m, 4°09'N/73°39'W, 8 XI 2002, 1 ex.

Distribution. Colombia; Costa Rica; Ecuador; Panama; Trinidad; Venezuela.

***Physonota alutacea* Boheman, 1854**

Cundinamarca, Girardot, 150 m, 4°30'N/75°45'W, 24 XI 2001, 1 ex., D. Moreno; **Cundinamarca**, Guaduas, 1007 m, 5°04'12"N/74°35'52"W, 6 V 1999, 1 ex., O. Higuera & R. Quevedo; **Cundinamarca**, San Francisco, 1570 m, 4°58'N/74°17'W, 1 VII 1970, 1 ex. ab. cyrtodes Boh., A. Moreno; **Cundinamarca**, Tocaima, 400 m, 4°27'40"N/74°38'18"W, 17 V 1969, 1 ex., A. Guzmán, 11 VII 1972, 1 ex., W. Toncel, 28 III 1994, 1 ex., L. Sarmiento; **Guajira**, Riohacha, 47 m, 11°33'N/72°55'W, 16 X|II 1974, 1 ex., A. Alarcón; **Meta**, Villavicencio, 467 m, 4°09'N/73°39'W, 18 XI 1994, 1 ex., G. González; **Sucre**, San Marcos, Santa Inés, 29 m, 8°40'N/75°08'W, 26 VI 2003, 1 ex. ab. cyrtodes Boh., A. Díaz; **Sucre**, Sincelejo, 200 m, 9°18'N/75°24'W, 12 V 1972, 1 ex., J. Vargas; **Tolima**, Melgar, 323 m, 4°12'24"N/74°38'44"W, 6 VI 1999, 2 exx., J. Arbelaez & F. Betancourt; **Tolima**, Purificación, 310 m, 3°51'N/74°56'W, 1 VI 1972, 2 exx., R. Arenas.

Distribution. Colombia; Costa Rica; Ecuador; Guatemala; Honduras; Mexico; Nicaragua; Panama; Trinidad; Venezuela; USA: Texas.

***Physonota pellucida* Wagener, 1877**

Antioquia, Jericó, 1967 m, 5°47'39"N/75°47'23"W, 1996, 8 exx., C. Tamayo; **Cundinamarca**, Caqueza, 1746 m, 4°24'30"N/73°56'58"W, 5 XI 1994, 1 ex., T. Luis.

Distribution. Colombia; Costa Rica; Nicaragua.

***Plagiometriona boschmai* Spaeth, 1937b**

Antioquia, Andes, Farallones del Citará, 1780 m, 5°45'33"N/76°03'42"W, 13 III 1999, 1 ex., D. Betancur; **Antioquia**, Andes, vereda La Siria, 2100 m, 24 IX 2000, 2 exx., S. Gomez; **Antioquia**, Andes, vereda Quebrada, Arriba, La Siria, 2200 m, 14 III 1999, 1 ex.; **Antioquia**, Frontino, 1317 m, 6°47'02"N/76°07'53"W, VI 1990, 1 ex., G. Morales; **Antioquia**, Urrao, 1790 m, 6°18'56"N/76°07'58"W, VI 1982, 1 ex., R. Bernal.

Distribution. Bolivia; Colombia; Ecuador; Venezuela.

***Plagiometriona latemarginata* Borowiec, 2001**

Antioquia, Frontino, 1317 m, 6°46'N/76°08'W, VII 1989, 1 ex., G. Morales & C. Mantilla.

Distribution. Panama. **New to Colombia.**

***Plagiometriona pehlkei* Spaeth, 1912**

Boyacá, San Pedro de Iguaque, 2750 m, 5°38'N/73°31'W, 7 V 1988, 1 ex., Lara; **Boyacá**, Villa de Leyva, Vda. Capilla, 2143 m, 5°38'N/73°31'W, 2 VI 2001, 1 ex., V. Quintero; **Cundinamarca**, Gachetá, "La Cima", Fca. Bellavista, 1716 m, 4°55'N/73°51'W, 16 XI 2003, 1 ex., J. Lozano; **Cundinamarca**, La Mesa, 1298 m, 4°38'05"N/74°27'57"W, 14 III 1981, 1 ex., León & Garcia; **Cundinamarca**, La Mesa, Laguna Pedro Palo, 1298 m, 4°38'05"N/74°27'57"W, 2 XI 1996, 1 ex., A. Romero, 15 II 1997, 1 ex., P. Acosta, 16 XI 1997, 1 ex., D. Useche; **Cundinamarca**, La Vega, 1215 m, 4°59'57"N/74°20'23"W, 29 III 1994, 1 ex., D. Moro; **Cundinamarca**, La Vega, Vrda. San Francisco, 1215 m, 4°59'57"N/74°20'23"W, 28 IV 1999, 1 ex., D. Reynales; **Cundinamarca**, San Antonio del Tequendama, 1521 m, 4°37'04"N/74°21'15"W, 12 X 1998, 1 ex., G. Castañeda; **Cundinamarca**, Tena, 1384 m, 4°39'33"N/74°23'28"W, 1 ex., A. Tovar; **Cundinamarca**, Tena, El Ospicio, 1384 m, 4°39'33"N/74°23'28"W, 22 XI 1997, 1 ex., J. Martinez & D. Vanegas; **Cundinamarca**, Tibirita, 1980 m, 5°03'00"N/73°10'31"W, 22 XI 2003, 1 ex., O. Munar; **Cundinamarca**, Une, Puente Piedra Rosa, 2420 m, 4°24'N/74°02'W, 20 V 2001, 1 ex., D. Torres; **Huila**, Iquira, Potrerito, Finca La Victoria, 1123 m, 2°39'07"N/75°38'23"W, 29 VIII 2003, 1 ex., L. Martinez;

Meta, Villavicencio, 467 m, 4°09'N/73°39'W, 1 V 1995, 1 ex., E. Losano, 4 XI 2001, 1 ex., M. Guillén.

Distribution. Colombia; Venezuela.

***Plagiometriona perroudi* (Boheman, 1862)**

Boyacá, Villa de Leyva, Vda. Capilla, 5°38'N/73°31'W, 2143 m, 10 V 2001, 1 ex., V. Quintero.

Distribution. Colombia.

***Polychalca perforata* (Boheman, 1850)**

Antioquia, Col. Bosque, 2150 m, 6°59'N/75°57'W, 22 X 2007, 1 ex., D.J. Restrepo.

Distribution. Colombia.

***Polychalma multicava* (Latreille, 1811)**

Antioquia, Amalfi, Cañón del Porce, Calandria, 985 m, 6°46'49.61"N/75°05'53.1"W, 25 VI 1997, 1 ex., J.G. Hurtado; **Antioquia**, Amalfi, Cañón del Porce, Normandia, 1000 m, 6°46'15.9"N/75°06'11"W, II 1998, 1 ex., J.G. Hurtado; **Caldas**, La Dorada, 178 m, 5°27'24"N/74°40'02"W, 1 IV 1967, 1 ex., Alcaraz; **Casanare**, Nunchia, Paz, 440 m, 5°38'N/72°11'W, 1 IX 1967, 1 ex., E. Cotes; **Cesar**, Aguachica, 162 m, 8°18'42"N/73°27'03"W, 24 III 1989, 1 ex., M. Jiménez; **Cundinamarca**, Villeta, 842 m, 5°00'52"N/74°28'23"W, 2 V 1967, 1 ex., I. Giraldo, 15 VI 1967, 1 ex., A. Reyes, 16 IX 1973, 1 ex., M. Arevalo; **Magdalena**, Ciénaga, Cgto. Sevilla, 12 m, 11°00'N/74°15'W, 15 VI 1971, 1 ex., A. Martínez; **Meta**, San Martín, 419 m, 3°42'N/73°42'W, 28 IV 1989, 1 ex., C. Castillo; **Norte de Santander**, Cúcuta, 320 m, 7°53'N/72°30'W, 5 V 1973, 1 ex., A. Porras; **Santander**, Bucaramanga, 958 m, 7°07'N/73°07'W, 2 XI 1973, 1 ex., Castellano; **Sucre**, San Marcos, Santa Inés, 29 m, 8°40'N/75°08'W, 26 VI 2003, 1 ex., A. Díaz; **Tolima**, Mariquita, 328 m, 5°12'N/74°55'W, 12 III 1967, 1 ex., H. Reyes, 19 II 1971, 3 exx., 20 II 1971, 2 exx., G. Hurtado.

Distribution. Colombia; Costa Rica; Ecuador; Panama; Peru; Venezuela.

***Stolas blanda* (Boheman, 1850)**

Huila, Garzón, 828 m, 2°12'N/75°38'W, 4 I 1972, 1 ex., F. Ramírez.

Distribution. Brazil; Colombia; Ecuador.

***Stolas ephippium* (Lichtenstein, 1796)**

Santander, Landazuri, 1600 m, 6°13'N/79°45'W, VI 1984, 1 ex., Luengas.

Distribution. Brazil; Colombia; Costa Rica; Ecuador; Guatemala; Guyana; Nicaragua; Panama; Surinam.

***Stolas haematites* (Lichtenstein, 1796)**

Antioquia, Amalfi, Cañón del Porce, 1050 m, 6°46'N/75°05'W, 1997, 2 exx., J.G. Hurtado; **Antioquia**, Barbosa, 1308 m, 6°26'N/75°20'W, IX 1983, 1 ex., Barreiro; **Antioquia**, La Estrella, 1764 m, 6°09'N/75°39'W, XI 1981, 1 ex., B. Múnera; **Antioquia**, La Pintada, 682 m, 5°44'N/75°35'W, X 1971, 1 ex., R. Vélez; **Cundinamarca**, Mesitas del Colegio, 4°35'14"N/74°26'58"W, 7 X 1989, 1 ex., M. Beltrán; **Norte de Santander**, El Carmen, 761 m, 8°30'36"N/73°27'11"W, 15 III 1994, 1 ex.

Distribution. Brazil; Colombia; French Guyana; Paraguay: Presidente Hayes; Venezuela.

***Stolas lebasii* (Boheman, 1850)**

Valle del Cauca, Cali, 987 m, 3°26'N/76°31'W, 11 XI 1974, 1 ex., A. Contreras.

Distribution. Belize; Colombia; Costa Rica; Guatemala; Honduras; Mexico; Nicaragua; Panama; Trinidad.

***Stolas stolidus* (Spaeth, 1917)**

Cacuetá, Florencia, 480 m, 1°36'N/75°37'W, 12 VIII 1968, 1 ex., J. Bobadilla; **Cundinamarca**, Cachipay, 474 m, 5°16'22"N/74°34'22"W, 13 V 1977, 1 ex., E. de León; **Meta**, Acacias, 522 m, 4°00'N/73°46'W, 12 III 1977, 1 ex., A. Cubides; **Meta**, La Macarena, 3°11'16"N/73°59'20"W, 23 III 1997, 1 ex., F. Villarmil, 26 III 1997, 1 ex., E. Bastidas; **Meta**, Villavicencio, 467 m, 4°09'N/73°39'W, 10 V 1967, 1 ex., H. Ramos, 20 VI 1967, 1 ex., E. Peralta, VII 1967, 1 ex., P. Pérez.

Distribution. Colombia; Ecuador.

***Stolas tachiraensis* Borowiec, 2009b**

Boyacá, San Pedro de Iguaque, 2750 m, 5°38'N/73°31'W, 7 V 1988, 1 ex., G. Negret; **Cundinamarca**, Anolaima, 1726 m, 4°45'54"N/74°28'08"W, 15 IV 1992, 1 ex., I. García; **Cundinamarca**, Anolaima, Carretera vía a Anolaima, 1656 m, 4°45'N/74°28'W,

8 IV 1989, 1 ex., C. Garzón; **Cundinamarca**, Cachipay, Insp. Pol. Anolaima, 5°16'22"N/74°34'22"W, 30 VIII 1988, 1 ex., E. Rivera; **Cundinamarca**, Caqueza, 1746 m, 4°24'30"N/73°56'58"W, 5 XI 1994, 1 ex., T. Luis; **Cundinamarca**, Fusagasugá, 1746 m, 4°20'49"N/74°21'53"W, 15 III 1992, 1 ex., Ramos & Quiroga; **Cundinamarca**, Girardot, 281 m, 4°18'18"N/74°48'08"W, 28 XII 1985, 1 ex., Torres & Viña, 28 V 1992, 1 ex., L. Narvaez; **Cundinamarca**, Guayabal de Siquima, Vda. El Resguardo, 4°53'N/74°28'W, 1630 m, 2005, 1 ex., 1636 m, 2005, 1 ex., F. Cruz; **Cundinamarca**, **Cundinamarca**, La Mesa, 1298 m, 4°38'05"N/74°27'57"W, 24 V 1992, 1 ex., A. Ariza & L. Ferrucho, 4 II 1994, 1 ex., Ubaque, 1 IV 1997, 1 ex., J. Camargo; **Cundinamarca**, La Vega, 1230 m, 4°59'57"N/74°20'23"W, 2 IV 1967, 1 ex., Ardila; **Cundinamarca**, Mesitas del Colegio, San José, 983 m, 4°35'N/74°26'W, 16 III 1975, 1 ex., A. Martínez, 4 XII 2004, 1 ex., S. Cubillos; **Cundinamarca**, Quipile, 1444 m, 4°44'48"N/74°32'14"W, 4 V 1990, 1 ex., S. Suárez; **Cundinamarca**, Sylvania, 1470 m, 4°24'21"N/74°23'24"W, 3 X 1996, 1 ex., S. Fuentes; **Cundinamarca**, Villeta, 804 m, 5°00'52"N/74°28'23"W, 3 VI 1967, 1 ex., M. Contreras; **Meta**, Humadea Insp., Pol. Guamal, 518 m, 3°51'N/73°45'W, 6 V 1999, 1 ex., O. Higuera & R. Quevedo; **Meta**, Villavicencio, 467 m, 4°09'N/73°39'W, 25 X 1988, 1 ex., P. León; **Santander**, Barbosa, Cite Las Delicias, 1600 m, 5°53'N/73°34'W, 28 VIII 2004, 1 ex., D. Mejía, 1 ex., E. Villarraga, 20 IX 2004, 1 ex., C. Soto; **Tolima**, Ibagué, 1285 m, 4°26'50"N/75°14'44"W, 1 ex., González & Nortua; **Tolima**, Mariquita, 328 m, 5°12'10"N/74°55'49"W, 14 X 1995, 1 ex., Carlos.

Distribution. Venezuela. **New to Colombia.**

Trilaccodea tomentosa (Boheman, 1850)

Antioquia, Medellín, 1538 m, 6°13'N/75°34'W, IX 1944, 1 ex., F.L. Gallego; **Boyacá**, Duitama, 2530 m, 5°49'35"N/73°02'32"W, 15 IV 1996, 1 ex., S. Alfonso; **Boyacá**, Tibaná, 2090 m, 5°19' 13"N/73°23'59"W, 20 IV 1996, 1 ex., 10 V 1996, 2 ex., B. Velandia; **Valle del Cauca**, Cali, 987 m, I. 1944, 1 ex., F. Gallego.

Distribution. Colombia; Venezuela.

Checklist of tortoise beetles of Colombia

[endemic species and department data in bold, uncertain and imprecise location in normal and in square brackets; colour photos of species marked with an asterisk (*) are available on web page by Borowiec and Świętojańska (2014)]

Tribe Cassidini

Agroiconota judaica* (Fabricius, 1781) – **Antioquia, **Bolivar**, **Boyacá**, **Cesar**, **Córdoba**, **Cundinamarca**, **Meta**, **Norte de Santander**, **Santander**, **Tolima**, **Valle del Cauca**

- **Agroiconota propinqua* (Boheman, 1855) – **Antioquia, Atlántico, Bolivar, Caldas, Casanare, Chocó, Cundinamarca, Magdalena, Meta, Tolima**
- **Agroiconota sodalis* Spaeth, 1936a – [Rio Magdalena]
- **Aidoia nubilosa* Boheman, 1855 – **Cundinamarca**
- **Charidotella amricula* (Spaeth, 1936a) – **Valle del Cauca**
- **Charidotella balteata* (Champion, 1894) – **Antioquia**
- **Charidotella bifasciata* (Linnaeus, 1758) – **Norte de Santander**
- **Charidotella carnulenta* (Erichson, 1847) – **Caqueta, Meta**
- **Charidotella circumnotata* (Boheman, 1862) – **Antioquia, Huila, Santander**
- **Charidotella glaucovittata* (Erichson, 1847) – **Cundinamarca, Meta, Valle del Cauca**
- **Charidotella immaculata* (Olivier, 1790) – **Cundinamarca, Huila, Meta, Norte de Santander, Tolima**
- **Charidotella incorrupta* (Boheman, 1855) – **Antioquia, Cundinamarca, Meta, Tolima**
- **Charidotella liquida* (Erichson, 1847) – **Cundinamarca, Meta**
- **Charidotella moraguesi* Borowiec, 2007b – **Tolima**
- **Charidotella myops* (Boheman, 1855) – [Colombia]
- Charidotella oblectabilis* (Spaeth, 1926a) – [Colombia]**
- **Charidotella puella* (Boheman, 1855) – **Antioquia, Bolivar, Boyacá, Cesar, Cundinamarca, Meta, Tolima, Valle del Cauca**
- **Charidotella purpurea* (Linnaeus, 1758) – [Colombia]
- **Charidotella sexpunctata* (Fabricius, 1781) – **Antioquia, Cundinamarca, Huila, Meta, Santander, Tolima, Valle del Cauca**
- **Charidotella tuberculata* (Fabricius, 1775) – **Magdalena, Meta, Tolima**
- **Charidotella vinula* (Boheman, 1855) – **Cundinamarca, Valle del Cauca**
- **Charidotis aurofasciata* (Erichson, 1847) – [Colombia]
- **Charidotis bipartita* (Boheman, 1855) – **Santander**
- **Charidotis cincticula* (Boheman, 1855) – **Cundinamarca**
- Charidotis discicollis* Boheman, 1855 – [Colombia]**
- **Charidotis exigua* Boheman, 1855 – [Colombia]
- **Charidotis furva* Boheman, 1855 – **Norte de Santander**
- Charidotis languida* Spaeth, 1936b – [Colombia]**
- **Charidotis luteola* Boheman, 1855 – [Colombia]
- **Charidotis vitreata* (Perty, 1830) – **Antioquia, Boyacá**
- **Chersinellina heteropunctata* (Boheman, 1854) – **Córdoba, Cundinamarca, Magdalena**
- Coptocyclus* sp. near *rufonotata* Sekerka & Windsor in litt. – **Antioquia, Magdalena**
- **Coptocyclus robusta* Spaeth, 1936c – [Colombia]
- **Cteisella centropunctata* (Boheman, 1855) [Colombia]
- **Cteisella divalis* Spaeth, 1926b – **Cundinamarca, Tolima**
- **Cyclocassis secunda* Borowiec, 1998a – **Norte de Santander**
- **Deloyala fuliginosa* (Olivier, 1790) – **Córdoba, Valle del Cauca**
- **Deloyala insubida* (Boheman, 1855) – **Antioquia, Cundinamarca, Meta, Tolima, Valle del Cauca**
- **Helocassis crucipennis* (Boheman, 1855) – **Sucre**

- **Helocassis testudinaria* (Boheman, 1855) – **Antioquia, Cundinamarca**
- **Hybosa galbanata* Boheman, 1855 – **Caldas**
- Hybosa unicolor* Wagener, 1877 – [Colombia]
- **Ischnocodia annulus* (Fabricius, 1781) – **Cundinamarca, Meta, Norte de Santander, Santander, Tolima, Valle del Cauca**
- **Metrionella erratica* (Boheman, 1855) – [Colombia]
- **Metrionella placans* Spaeth, 1932 – [Colombia - Cachabé; now the locality is in Esmeralda Province in Ecuador close to Colombian border thus occurrence of this species in recent Colombia needs confirmation]
- **Metrionella tumacoensis* Borowiec, 2002b – **Nariño**
- Microtenochira arcana* (Spaeth, 1926b) – [Colombia – Nova Granada]
- **Microtenochira aspersa* (Champion, 1894) – **Antioquia, Cundinamarca, Magdalena, Meta, Santander**
- **Microtenochira bifenestrata* (Boheman, 1855) – **Cundinamarca**
- Microtenochira bogotana* (Spaeth, 1926b) – **Cundinamarca**
- **Microtenochira cumulata* (Boheman, 1855) – **Antioquia**
- **Microtenochira diffinis* (Boheman, 1855) – **Antioquia, Amazonas, Cundinamarca**
- **Microtenochira fairmairei* (Boheman, 1855) – **Antioquia**
- **Microtenochira flavonotata* (Boheman, 1855) – **Cundinamarca**
- **Microtenochira fraterna* (Boheman, 1855) – **Antioquia, Boyacá, Cundinamarca, Valle del Cauca**
- Microtenochira impolluta* (Spaeth, 1926b) – **Antioquia**
- **Microtenochira jousselini* (Boheman, 1855) – **Boyacá**
- **Microtenochira libidinosa* (Spaeth, 1926b) – **Valle del Cauca**
- **Microtenochira lindigi* (Kirsch, 1865) – **Antioquia, Cundinamarca, Meta**
- **Microtenochira lugubris* (Boheman, 1862) – [Colombia]
- **Microtenochira nigrocincta* (Wagener, 1877) – **Bolivar**
- **Microtenochira peltata* (Boheman, 1855) – **Cundinamarca**
- **Microtenochira porosa* (Boheman, 1855) – **Cundinamarca**
- **Microtenochira quadrata* (DeGeer, 1775) – **Antioquia, Cundinamarca, Meta**
- **Microtenochira reticularis* (DeGeer, 1775) – **Antioquia, Cundinamarca, Putumayo**
- **Microtenochira rubrocincta* (Boheman, 1855) – [Colombia]
- Microtenochira semifasciata* (Boheman, 1855) – [Colombia]
- **Microtenochira semilobata* (Wagener, 1877) – **Antioquia**
- **Microtenochira semilunaris* (Boheman, 1862) – **Antioquia, Boyacá, Cundinamarca, Meta**
- **Microtenochira sepulchralis* (Boheman, 1855) – **Antioquia, Cundinamarca**
- **Microtenochira sertata* (Erichson, 1847) – **Antioquia, Bolivar, Boyacá, Córdoba, Cundinamarca, Meta, Putumayo, Valle del Cauca**
- Nuzonia ibaguensis* Spaeth, 1912 – **Tolima**
- **Nuzonia marginepunctata* Borowiec, 2000 – **Caldas, Valle del Cauca**

- **Orexita blattoides* Spaeth, 1911 – [Colombia]
 Orexita justini* (Boheman, 1855) – **Cundinamarca
 **Orexita plagipennis* Spaeth, 1911 – [Colombia]
 Orexita subgibbosa* Spaeth, 1911 – **Valle del Cauca
 Parachirida flavolineata* (Latreille, 1811) – **Bolivar, Santander
 Parachirida semiannulata* (Boheman, 1855) – **Antioquia, Cundinamarca
 Parachirida subirrorata* (Boheman, 1855) – **Córdoba, Meta
Plagiometriona aucta (Boheman, 1855) – [Colombia]
Plagiometriona bisbimaculata (Boheman, 1855) – [Colombia]
 Plagiometriona boschmai* Spaeth, 1937b – **Antioquia, Cundinamarca, Tolima, Valle del Cauca
 Plagiometriona buqueti* (Boheman, 1855) – **Boyacá, Cundinamarca, Tolima
Plagiometriona columbica Spaeth, 1937b – [Colombia]
Plagiometriona fragilicornis Spaeth, 1937b – **Tolima**
Plagiometriona glyphica (Boheman, 1855) – **Tolima**
 Plagiometriona latemarginata* Borowiec, 2001 – **Antioquia
Plagiometriona nobilis Spaeth, 1937b – **Tolima**
 Plagiometriona pehlkei* Spaeth, 1912 – **Boyacá, Cundinamarca, Huila, Meta, Tolima
 Plagiometriona pernix* Spaeth, 1912 – **Tolima
 Plagiometriona perroudi* (Boheman, 1862) – **Boyacá, Cauca, Cundinamarca
 Plagiometriona phoebe* (Boheman, 1855) – **Antioquia, Boyacá
Plagiometriona ramosa (Boheman, 1855) – [Colombia]
Plagiometriona resplendens (Kirsch, 1865) – **Cundinamarca**
 Plagiometriona steinheili* (Wagener, 1877) – **Norte de Santander
 Plagiometriona zelleri* (Boheman, 1855) – **Boyacá, Cundinamarca

Tribe Delocraniini

- **Delocrania cossyphoides* Guérin, 1844 – **Magdalena, Santander**

Tribe Dorynotini

- **Dorynota electa* (Spaeth, 1923) – **Risaralda**
Dorynota hastifera (Spaeth, 1923) – [Colombia]
 **Dorynota insidiosa* (Boheman, 1854) – [Colombia]
 Dorynota kiesenwetteri* (Boheman, 1854) – **Meta
 Dorynota nodosa* (Boheman, 1854) – **Sucre
Dorynota rufomarginata (Wagener, 1881) – **Meta**
 **Dorynota truncata* (Fabricius, 1781) – [Colombia]

Tribe Eugenysini

- **Agenysa connectens* (Baly, 1869) – **Antioquia, Huila**
- **Agenysa crassicornis* Spaeth, 1905 – **Risaralda, Santander**
- **Eugenysa columbiana* (Boheman, 1850) – **Antioquia, Bolivar, Boyacá, Caldas, Cundinamarca, Valle del Cauca**
- **Eugenysa martae* Borowiec, 1987 – **Valle del Cauca**
- **Eugenysa regalis* (Boheman, 1850) – [Colombia]
- **Eugenysa unicolor* Borowiec & Dąbrowska, 1997 – **Cesar**
- **Miocalaspis gentilis* (Erichson, 1847) – [Colombia]

Tribe Goniocheniini

- **Chlamydocassis bicornuta* (Boheman, 1850) – [Colombia]
- **Goniochenia buckleyi* (Baly, 1872) – [Colombia]
- **Goniochenia elocata* (Boheman, 1850) – **Antioquia, Valle del Cauca, Tolima**
- **Polychalma multicava* (Latreille, 1811) – **Antioquia, Boyacá, Caldas, Casanare, Cesar, Cundinamarca, Magdalena, Meta, Norte de Santander, Sucre, Tolima, Valle del Cauca**

Tribe Hemisphaerotini

- **Spaethiella circumdata* (Boheman, 1850) – **Bolivar, Cundinamarca**
 - **Spaethiella coccinea* (Boheman, 1850) – **Amazonas, Meta**
 - Spaethiella flexuosa* (Champion, 1893) – **Magdalena**
 - **Spaethiella laevicollis* (Spaeth, 1910) – **Tolima**
 - **Spaethiella miniata* (Boheman, 1856) – [Colombia]
 - **Spaethiella pulchella* (Baly, 1859) – [Colombia]
 - Spaethiella purpureocincta* (Spaeth, 1929) – **Cundinamarca**
 - **Spaethiella quadrata* (Spaeth, 1902) – **Caquetá**
 - **Spaethiella robusta* (Spaeth, 1910) – **Norte de Santander, Tolima**, [Colombia – Villa Carolina, Villa Elvira]
 - **Spaethiella sanguinea* (Fabricius, 1801) – [Colombia]
 - **Spaethiella sublaevis* (Spaeth, 1901) – **Valle del Cauca**
 - **Spaethiella valida* (Spaeth, 1901) – **Valle del Cauca**
- Tribe Mesomphaliini
- **Acromis sparsa* (Boheman, 1854) – **Antioquia, Boyacá, Cundinamarca, Norte de Santander, Santander, Tolima, Valle del Cauca**
 - **Acromis spinifex* (Linnaeus, 1763) – [Colombia]
 - **Acromis venosa* (Erichson, 1847) – [Colombia]
 - **Botanochara ordinata* (Boheman, 1850) – **Santander**

- **Chelymorpha alternans* Boheman, 1854 – **Nariño**
***Chelymorpha atomaria* Boheman, 1854** – [Colombia]
 Chelymorpha cavata* Boheman, 1854 – **Antioquia, Cundinamarca
 Chelymorpha cribraria* (Fabricius, 1775) – **Antioquia, Boyacá, Valle del Cauca
 Chelymorpha infirma* Boheman, 1854 – **Huila
 Chelymorpha marginata* (Linnaeus, 1758) – **Cesar, Cundinamarca, Meta
 Chelymorpha praetextata* Boheman, 1854 – **Boyacá
***Chelymorpha stygia* Boheman, 1862** – **Cundinamarca**
 Chelymorpha testaceomarginata* Boheman, 1854 – **Boyacá, Cundinamarca, Huila, Meta, Norte de Santander, Tolima, Valle del Cauca
 Chelymorpha variolosa* (Olivier, 1790) – **Antioquia
 ****Cyrtonota abrili* Borowiec & Świętojańska sp. n.** – **Antioquia, Caldas**
 Cyrtonota balyi* (Kirsch, 1883) – **Putumayo
 ****Cyrtonota bergeali* Borowiec & Sassi, 1999** – **Valle del Cauca**
 ****Cyrtonota bugaensis* Borowiec & Sassi, 1999** – **Valle del Cauca**
 ****Cyrtonota caudata* (Boheman, 1850)** – **Caldas, Cesar, Risaralda, Tolima**
 ****Cyrtonota compulsa* (Spaeth, 1909)** – **Tolima**
 Cyrtonota dissecta* (Boheman, 1850) – **Cundinamarca, Meta, Risaralda, Tolima
 ****Cyrtonota gibbera* Borowiec, 1989** – **Cundinamarca**
 ****Cyrtonota goryi* (Boheman, 1850)** – **Meta, Tolima**
 Cyrtonota kolbei* (Spaeth, 1907) – **Huila
 ****Cyrtonota lurida* (Spaeth, 1913)** – [Colombia]
 ****Cyrtonota moderata* (Spaeth, 1913)** – **Caldas, Quindio**
 ****Cyrtonota pavens* (Spaeth, 1913)** – [Colombia]
 ****Cyrtonota pyramidata* (Boheman, 1850)** – [Colombia]
 ****Cyrtonota santanderensis* Borowiec, 2009a** – **Santander**
 Cyrtonota serinus* (Erichson, 1847) – **Amazonas, Huila
 Cyrtonota steinheili* (Wagener, 1877) – **Cundinamarca, Toledo
 ****Cyrtonota textilis* (Boheman, 1850)** – **Cundinamarca, Nariño**
 **Cyrtonota tigrina* (Boheman, 1850) – [Colombia]
 ****Cyrtonota timida* Sassi, 2008** – **Nariño**
 ****Echoma anaglypta* (Boheman, 1862)** – [Colombia]
 ****Echoma anaglyptooides* Borowiec, 1998b** – **Antioquia, Cundinamarca, Tolima, Valle del Cauca**
 ****Echoma clypeata* (Panzer, 1798)** – **Antioquia, Meta**
 ****Echoma signata* (Panzer, 1798)** – **Antioquia, Cundinamarca**
 ****Hilarocassis bordoni* Borowiec, 2002a** – **Cundinamarca**
 ****Hilarocassis evanida* (Boheman, 1850)** – [Colombia; occurrence of this species in Colombia needs confirmation because with great probability based on misidentification with *Hilarocassis bordoni* Borowiec]
 ****Omaspides augusta* Boheman, 1856** – [Colombia – Rio Tacana]
 ****Omaspides bistrinata* Boheman, 1862** – **Valle del Cauca**
***Omaspides limbipennis* Spaeth, 1922** – **Meta**

- **Omaspides nitidicollis* Spaeth, 1937a – **Antioquia, Caldas, Santander, Tolima, Valle del Cauca**
- **Omaspides specularis* (Erichson, 1847) – **Meta, Valle del Cauca**
- **Paraselenis nupta* (Boheman, 1854) – **Cundinamarca**
- **Paraselenis tersa* (Boheman, 1854) – [Colombia]
- **Stolas bioculata* (Boheman, 1850) – [Colombia]
- **Stolas blanda* (Boheman, 1850) – **Huila, Meta, Tolima**
- **Stolas coerulea* (Boheman, 1850) – **Antioquia**
- **Stolas decemguttata* (Sturm, 1828) – [Colombia]
- **Stolas discoides* (Linnaeus, 1758) – [Colombia]
- **Stolas ephippium* (Lichtenstein, 1796) – **Antioquia, Santander, Valle del Cauca**
- **Stolas excelsa* (Spaeth, 1917) – **Valle del Cauca**
- **Stolas extricata* (Boheman, 1850) – **Bolivar, Valle del Cauca**
- **Stolas haematites* (Lichtenstein, 1796) – **Antioquia, Cundinamarca, Norte de Santander**
- **Stolas inexculta* (Boheman, 1862) – **Risaralda**
- **Stolas lebasii* (Boheman, 1850) – **Valle del Cauca**
- **Stolas napoensis* Borowiec, 1998a – **Risaralda**
- **Stolas niobe* (Spaeth, 1919a) – **Risaralda**
- **Stolas pertusa* (Boheman, 1850) – [Colombia]
- **Stolas pleurosticha* (Erichson, 1847) – **Valle del Cauca**
- **Stolas puberula* (Boheman, 1856) – **Huila, Risaralda**
- **Stolas quinquefasciata* (Wagener, 1877) – [Colombia]
- **Stolas rubroreticulata* (Boheman, 1856) – **Boyacá, Cundinamarca, Tolima**
- **Stolas stolidia* (Spaeth, 1917) – **Cacuetá, Cundinamarca, Huila, Meta**
- **Stolas tachiraensis* Borowiec, 2009b – **Boyacá, Cundinamarca, Meta, Santander, Tolima**
- **Trilaccodea excisa* (Boheman, 1856) – [Colombia]
- **Trilaccodea tomentosa* (Boheman, 1850) – **Antioquia, Boyacá, Valle del Cauca**
- **Zatrephina lineata* (Fabricius, 1787) – [Colombia]

Tribe Omocerini

- **Canistra osculatii* Guérin, 1855 – **Antioquia, Huila, Risaralda, Tolima**
- **Canistra varicosa* Erichson, 1847 – **Valle del Cauca**
- **Discomorpha amazona* (Spaeth, 1940) – **Meta, Santander**
- **Discomorpha batesi* (Boheman, 1856) – **Antioquia**
- **Discomorpha bernhaueri* (Spaeth, 1909) – **Valle del Cauca**
- **Discomorpha biplagiata* (Guérin, 1844) – **Bolivar, Casanare, Cundinamarca, Huila, Tolima, Valle del Cauca**
- Discomorpha breiti* (Spaeth, 1907) – [Colombia]
- **Discomorpha conspersipennis* (Boheman, 1862) – **Antioquia, Bolivar, Cundinamarca**
- Discomorpha garitana* (Spaeth, 1919b) – **Norte de Santander**

- ****Discomorpha giganteensis* Borowiec, 2006a – Huila**
 Discomorpha instabilis* (Baly, 1872) – **Cundinamarca, Huila, Tolima
 **Discomorpha languinosa* (Boheman, 1850) – [Colombia]
 Discomorpha mandli* (Spaeth, 1909) – **Huila
 Discomorpha miniata* (Boheman, 1850) – **Antioquia, Huila, Putumayo
 Discomorpha nigropunctata* (Boheman, 1850) – **Boyacá, Valle del Cauca
***Discomorpha nigrosanguinea* (Wagener, 1877) – Tolima**
 Discomorpha nigrosparsa* (Wagener, 1877) – **Caldas, Valle del Cauca
 Discomorpha panamensis* (Spaeth, 1919b) – **Antioquia
 Discomorpha peruviana* (Boheman, 1850) – **Meta
 **Discomorpha salvini* (Baly, 1864) – [Colombia]
***Discomorpha skalitzkyi* (Spaeth, 1911) – [Colombia]**
 ****Discomorpha spectanda* (Boheman, 1862) – Magdalena**
 Discomorpha waehneri* (Spaeth, 1940) – **Huila, Putumayo
 ****Discomorpha wingelmuelleri* (Spaeth, 1907) – [Colombia]**
 **Omocerus casta* (Boheman, 1862) – [Colombia]
***Omocerus caucanus* (Spaeth, 1931) – Valle del Cauca**
 Omocerus creberrimus* (Boheman, 1850) – **Antioquia, Cundinamarca
 **Omocerus reichei* (Boheman, 1850) – [Colombia; occurrence of this species in Colombia needs confirmation because with great probability based on misidentification]
Omocerus relucens (Spaeth, 1931) – **Cordoba**
 Omocerus smaragdinus* (Boheman, 1850) - **Meta
 **Omocerus taurus* (Fabricius, 1787) – [Colombia]
Omocerus viridicoeruleus (Boheman, 1850) – [Colombia]
 ****Polychalca perforata* (Boheman, 1850) – Antioquia, Boyacá, Cundinamarca**

Tribe Physonotini

- **Cistudinella foveolata* Champion, 1894 – **Guaviare**
 Eurypedus nigrosignatus* (Boheman, 1854) – **Atlántico, Caldas, Casanare, Cundinamarca, Huila, Magdalena, Meta, Norte de Santander, Tolima
 Physonota alutacea* Boheman, 1854 – **Cundinamarca, Guajira, Meta, Sucre, Tolima
 Physonota lutarella* Boheman, 1856 – **Boyacá, Valle del Cauca, Tolima
 ****Physonota pellucida* Wagener, 1877 – Antioquia, Cundinamarca**
***Physonota plana* Boheman, 1854 – Cundinamarca**

Discussion

South America with approximately 2/3 of described world cassids is a centre of diversity of tortoise beetles (Borowiec 1999, Borowiec and Świętojańska 2014a). Until recently only three complete checklists of species supplemented by new faunistic materials were

published for Neotropical countries: Ecuador (Borowiec 1998a), Trinidad and Tobago (Chaboo and Borowiec 2003) and French Guyana (Borowiec and Moragues 2005), including descriptions of several species new to science (193, 38 and 121 species of tortoise beetles were recorded respectively). The lists and catalogue cited above suggest that western Andean countries (from Colombia to Bolivia) might have several endemic species. Summarized data of distribution of Neotropical tortoise beetles in the web page by Borowiec and Świętojańska (2014b) show that, among the Andean countries, the richest is the fauna of Peru – 323 species, being 81 endemics (25.1%), followed by Bolivia – 254 species, with 42 endemics (16.5%), and Ecuador – 214 species, with 63 endemics (29.4%). The present contribution presents 238 species and 60 endemics (25.2%), but we anticipate many more species since Colombia is much larger than Ecuador yet the two countries have similar numbers of recorded species. Out of the 238 listed species recorded from Colombia 62 (26.1%) still have imprecise location.

Acknowledgments

We would like to express our gratitude to Erika Valentina Vergara Navarro, the curator of the Museo Entomológico UNAB, Universidad Nacional de Colombia, Bogotá for the loan of materials. Thanks also to Lukáš Sekerka (Czech Republic) for his help in determination of some taxa and information about type of *Mesomphalia pyramidata* Boheman, 1850. The manuscript was improved significantly through critical readings by three anonymous reviewers. This paper was supported by the University of Wrocław, scientific support DS/IZ/2013.

References

- Baly JS (1859) Descriptions of new species of phytophagous insects. Transactions of the Entomological Society of London 1859: 146–161.
- Baly JS (1864) Descriptions of uncharacterized genera and species of Phytophaga. Transactions of the Entomological Society of London 1864: 223–243.
- Baly JS (1869) Characters of some undescribed species of Phytophaga belonging to the families Cassididae and Hispididae. Transactions of the Entomological Society of London 1869: 83–90.
- Baly JS (1872) Descriptions of some species of Cassididae new to science. Transactions of the Entomological Society of London 1872: 59–72.
- Boheman CH (1850) Monographia Cassidarum. Tomus primus. Holmiae, 452 pp. + 4 tab. doi: 10.5962/bhl.title.8973
- Boheman CH (1854) Monographia Cassidarum. Tomus secundus. Holmiae, 506 pp. + 2 tab.
- Boheman CH (1855) Monographia Cassidarum. Tomus tertius. Holmiae, 543 pp. + 1 tab.
- Boheman CH (1856) Catalogue of Coleopterous Insects in the collection of the British Museum, Part IX, Cassididae. London.

- Boheman CH (1862) Monographia Cassidarum. Tomus quartus. Holmiae, 504 pp.
- Borowiec L (1987) A new species of *Eugenysa* Chevrolat from Colombia (Coleoptera, Chrysomelidae, Cassidinae). *Polskie Pismo Entomologiczne* 56: 883–885.
- Borowiec L (1989) Two new species of *Cyrtonota* Chevrolat (Coleoptera, Chrysomelidae, Cassidinae). *Elytron* 3: 25–30.
- Borowiec L (1995) Tribal classification of the cassidoid Hispinae (Coleoptera: Chrysomelidae). In: Pakaluk J, Ślipiński SA. *Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson*, Warszawa, 541–558.
- Borowiec L (1996) Faunistic records of Neotropical Cassidinae (Coleoptera: Chrysomelidae). *Polskie Pismo Entomologiczne* 65: 119–251.
- Borowiec L (1998a) Review of the Cassidinae of Ecuador, with a description of thirteen new species (Coleoptera: Chrysomelidae). *International Journal of Invertebrate Taxonomy - Genus* 9: 155–246.
- Borowiec L (1998b) *Echoma anaglypta* (Boheman, 1862) and *E. anaglyptoidea* n. sp. (Coleoptera: Chrysomelidae: Cassidinae). *International Journal of Invertebrate Taxonomy - Genus* 9: 375–385.
- Borowiec L (1999) A world catalogue of the Cassidinae (Coleoptera: Chrysomelidae). *Biologica Silesiae*, Wrocław, 476 pp.
- Borowiec L (2000) Three new species of *Nuzonia* Spaeth, 1912 (Coleoptera: Chrysomelidae: Cassidinae). *International Journal of Invertebrate Taxonomy - Genus* 11: 59–67.
- Borowiec L (2001) Two new species of *Plagiometriona* Spaeth from Costa Rica and Panama (Coleoptera: Chrysomelidae: Cassidinae). *International Journal of Invertebrate Taxonomy - Genus* 12: 353–359.
- Borowiec L (2002a) New records of Neotropical Cassidinae, with description of three new species (Coleoptera: Chrysomelidae). *International Journal of Invertebrate Taxonomy - Genus* 13: 43–138.
- Borowiec L (2002b) *Mettrionella tumacoensis*, a new species from Colombia (Coleoptera: Chrysomelidae: Cassidinae). *International Journal of Invertebrate Taxonomy - Genus* 13: 139–142.
- Borowiec L (2006) Four new species of *Discomorpha* Chevrolat, 1837 (Coleoptera: Chrysomelidae: Cassidinae: Omocerini), with a key to *Discomorpha* s. str. *Zootaxa* 1357: 45–60.
- Borowiec L (2007a). A new species of *Cyrtonota* Chevrolat from Peru and note on *Cyrtonota balyi* (Kirsch, 1883) (Coleoptera: Chrysomelidae: Cassidinae: Stolaini). *Genus* 18: 477–485.
- Borowiec L (2007b) Two new species of *Charidotella* Weise (Coleoptera: Chrysomelidae: Cassidinae: Cassidini), with a key to *Charidotella sexpunctata* group. *Zootaxa* 1586: 59–66.
- Borowiec L (2009a) A new species of *Cyrtonota* Chevrolat from Colombia (Coleoptera: Chrysomelidae: Cassidinae: Mesomphaliini). *International Journal of Invertebrate Taxonomy - Genus* 20: 111–116.
- Borowiec L (2009b) New records of Neotropical tortoise beetles (Coleoptera: Chrysomelidae: Cassidinae). *International Journal of Invertebrate Taxonomy - Genus* 20: 615–722.
- Borowiec L, Dąbrowska A (1997) Two new species of *Eugenysa* Chevrolat, 1837 from Ecuador and Peru (Coleoptera: Chrysomelidae: Cassidinae). *International Journal of Invertebrate Taxonomy - Genus* 8: 673–678.

- Borowiec L, Moragues G (2005) Tortoise beetles of the French Guyana - a faunistic review (Coleoptera: Chrysomelidae: Cassidinae). *Genus* 16: 247–278.
- Borowiec L, Opalińska S (2007) The structure of the spermathecae of selected genera of Stollini and Eugenyini (Coleoptera: Chrysomelidae: Cassidinae) and its taxonomic significance. *Annales Zoologici* 57: 463–479.
- Borowiec L, Sassi D (1999) Four new species of *Cyrtanota* Chevrolat (Coleoptera: Chrysomelidae: Cassidinae). *International Journal of Invertebrate Taxonomy - Genus* 10: 89–101.
- Borowiec L, Świątojańska J (2014a) Cassidinae Gyllenhal, 1813. In: Richard AB, Leschen R, Beutel G (Eds) *Handbook of Zoology, Arthropoda, Insecta, Coleoptera, Beetles. Vol. 3: Morphology and Systematics (Phytophaga)*, De Gruyter, Berlin/Boston, 198–217.
- Borowiec L, Świątojańska J (2014b) Cassidinae of the world - an interactive manual (Coleoptera: Chrysomelidae). <http://www.biol.uni.wroc.pl/cassidae/katalog%20internetowy/index.htm> [last modification 17 XII 2014]
- Chaboo CS, Borowiec L (2003) Annotated checklist of tortoise beetles of Trinidad and Tobago (Coleoptera: Chrysomelidae: Cassidinae). *Coleopterists Bulletin* 57: 71–78. doi: 10.1649/0010-065X(2003)057[0071:ACOTBO]2.0.CO;2
- Champion GC (1893–1894) *Biologia Centrali-Americana. Insecta. Coleoptera. Vol. VI. Part 2. Phytophaga. Cassididae and appendix to Hispidae* 1893: 125–164, 1894: 165–249, tab. 5–13.
- Chevrolat LAA in Dejean PFMA (1837) *Catalogue des Coléoptères de la collection de M. le Comte Dejean, Troisième édition, revue, corrigée et augmentée*. Paris, livr. 5, 385–503.
- Degeer C (1775) *Mémoires pour servir à l'histoire des Insectes. V*. Stockholm, 448 pp. + 16 pl.
- Erichson GF (1847) *Conspectus Insectorum Coleopterorum, quae in Republica Peruana observata sunt*. *Archiv für Naturgeschichte* 13: 67–185.
- Fabricius JCh (1775) *Systema Entomologiae, sistens Insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus*. *Officina Libraria Kortii, Flensburgi et Lipsiae*, 32 + 832 pp. doi: 10.5962/bhl.title.36510
- Fabricius JCh (1781) *Species Insectorum eorum differentias specificas, synonyma auctorum, loca natalia, metamorphosis adiectis observationibus, descriptionibus. I. Hamburgi et Kilonii*, VIII + 552 pp.
- Fabricius JCh (1787) *Mantissa Insectorum sistens eorum species nuper detectas adiectis characteribus genericis, differentiis specificis, emendationibus, observationibus. I. Hafniae*, XX + 348 pp.
- Fabricius JCh (1801) *Systema Eleutheratorum secundum ordines, genera, species adiectis synonymis, locis, observationibus, descriptionibus. I. Bibliopolii Academici Novi, Kiliae*, XXIV + 506 pp.
- Guérin[-Méneville] FE (1844) *Iconographie du regne animal de G. Cuvier, ou représentation d'après nature de l'une des espèces les plus remarquables et souvent non encore figurées de chaque genre d'animaux, pouvant servir d'atlas à tous les traités de zoologie*. Paris, Vol. 7, 111 pl.
- Guérin[-Méneville] MFE (1855) *Catalogue des insectes coléoptères, recueillis par M. Gaetano Osculati, pendant son exploration de la région équatoriale, sur les bords du Napo et de l'Amazone*. *Verhandlungen des Zoologisch-Botanischen Vereins Wien* 5: 573–612.

- Kirsch T (1865) Beiträge zur Käferfauna von Bogota. Berliner Entomologische Zeitschrift 9: 40–104.
- Kirsch T (1883) Neue südamerikanische Käfer. Berliner Entomologische Zeitschrift 27: 187–213. doi: 10.1002/mmnd.18830270205
- Latreille PA (1811) Insectes de l'Amérique Equinoxiale, recueillis pendant le voyage de MM. de Humboldt et Bonpland. Paris, 127–252, pl. XV–XXV.
- Lichtenstein AAH (1796) Catalogus musei zoologici ditissimi Hamburgi, d. III Februar. 1796 auctionis lege distrahendi. Sectio Tertia. Continentes Insecta. 13, Schniebes, Hamburg, 224 pp.
- Linnaeus C (1758) Systema Naturae, sive regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio Decima, reformata. I. Holmiae, IV + 824 pp.
- Linnaeus C (1763) Amoenitates Academicæ seu Dissertationes variæ Physicæ, Medicæ Botanicae antehac seorsim editæ, nunc collectæ et auctæ cum tabulis æneis. Volumen sextum. Holmiae, 486 pp., 5 tt.
- Olivier AG (1790) Encyclopédie Méthodique, Histoire Naturelle. Insectes. Tome cinquième. Paris, 368 pp.
- Panzer GW (1798) Voets Beschreibungen und Abbildungen hartschaaligter Insecten, Coleoptera Linn. Aus dem Original getreu übersetzt, mit der in selbigem fehlenden Synonymie und beständigem Commentar versehen von D. Georg Wolfgang Franz Panzer. Th. 4, Erlangen, Palm, 112 pp. + 25 pl.
- Perty M (1830–1834) Delectus animalium articulorum, quæ in itinere per Brasiliam annis 1817–1820 jussu et auspiciis Maximiliani Josephi Bavarie regis augustissimi peracto, collegerunt Dr. J. B. de Spix et Dr. C. F. Ph. de Martius; digessit, descripsit et pingenda curavit Dr. M. Perty. Monachii, 4+44+222 pp.
- Sassi D (2008) *Cyrtanota timida*, a new species from Colombia (Coleoptera, Chrysomelidae, Cassidinae: Mesomphaliini). International Journal of Invertebrate Taxonomy - Genus 19: 291–295.
- Sekerka L (2007) Description of *Cyrtanota capribensis* n. sp. from Peru together with a redescription of *C. lurida* (Spaeth, 1913) (Coleoptera: Chrysomelidae: Cassidinae: Mesomphaliini). Genus 18: 671–676.
- Sekerka L (2014) Review of Imatidiini genera (Coleoptera: Chrysomelidae: Cassidinae). Acta Entomologica Musei Nationalis Pragae 54: 257–314.
- Spaeth F (1901) Beschreibung neuer Cassididen nebst synonymischen Bemerkungen. IV. Verhandlungen des Zoologisch-Botanischen Vereins Wien 51: 333–350.
- Spaeth F (1902) Neue Cassididen aus Peru. Deutsche Entomologische Zeitschrift 1902: 81–102.
- Spaeth F (1905) Beschreibung neuer Cassididen nebst synonymischen Bemerkungen. V. Verhandlungen des Zoologisch-Botanischen Vereins Wien 55: 79–118.
- Spaeth F (1907) Beschreibung neuer Cassididen nebst synonymischen Bemerkungen. VI. Verhandlungen des Zoologisch-Botanischen Vereins Wien 57: 137–166.
- Spaeth F (1909) Beschreibung neuer Cassididen nebst synonymischen Bemerkungen. VII. Verhandlungen des Zoologisch-Botanischen Vereins Wien 59: 364–397.
- Spaeth F (1910) Neue Arten der Gattung *Hemisphaerota* Spaeth (Col., Cassidae). Deutsche Entomologische Zeitschrift 1910: 55–62.

- Spaeth F (1911) Beschreibung neuer Cassididen nebst synonymischen Bemerkungen. VIII. Verhandlungen des Zoologisch-Botanischen Vereins Wien 61: 239–277.
- Spaeth F (1912) Neue Cassiden aus Columbien, Peru, Bolivien und Ecuador. Stettiner Entomologische Zeitung 73: 3–16.
- Spaeth F (1913) Kritische Studien über den Umfang und die Begrenzung mehrerer Cassidengattungen nebst Beschreibung neuer amerikan. Arten. Archiv für Naturgeschichte 79: 126–164.
- Spaeth F (1917) Beiträge zur Kenntnis der süd- und zentralamerikanischen Cassidinen. Coleopterologische Rundschau 6: 24–31.
- Spaeth F (1919a) Drei neue Cassidinen aus dem tropischen Amerika. Neue Beiträge zur systematischen Insektenkunde 1: 121–123.
- Spaeth F (1919b) Zur Kenntnis der Gattung *Oxymodera* (Col. Cassid.). Neue Beiträge zur systematischen Insektenkunde 1: 133–136.
- Spaeth F (1922) Neue Cassidinen (Coleoptera) des tropischen Amerika aus meiner und der Sammlung des zoologischen Museum in Kristiania. Norsk Entomologisk Tidsskrift 1: 165–181.
- Spaeth F (1923) Ueber *Batonota* Hope (Col. Cassid.). Wiener entomologische Zeitung 40: 65–76.
- Spaeth F (1926a) Beschreibung neuer Cassidinen, Bulletins mensuels de la Société des naturalistes luxembourgeois, N.S., 20: 11–24, 47–60.
- Spaeth F (1926b) Monographie der zur Gruppe der Coptocyclitae gehörigen amerikanischen Cassidinen (Col.): I. Die Gattungen mit gekamnten Klauen. Supplementa entomologica 13: 1–108.
- Spaeth F (1929) Die Gattung *Hemisphaerota* Spaeth (Coleopt. Chrysom. Cassid.). Koleopterologische Rundschau 15: 111–131.
- Spaeth F (1931) Über die Gattung *Tauroma* Hope (Col.). Stettiner Entomologische Zeitung 92: 305–314.
- Spaeth F (1932) Über die mit *Metriona erratica* verwandten Arten (Col., Chrysom. Cass.). Folia zoologica et hydrobiologica 4: 263–270.
- Spaeth F (1936a) Mitteilungen über neue oder bemerkenswerte Cassidinen aus dem Seneckberg-Museum (Ins. Col.). Entomologische Rundschau 53: 109–111, 138–140, 170–173, 213–216, 259–262.
- Spaeth F (1936b) Bestimmungstabelle der Gattung *Charidotis* (Col. Chrys. Cassid.). Sborník entomologického oddělení Národního muzea v Praze 126: 66–169.
- Spaeth F (1936c) Die Untergattungenvon *Coptocycla* mit gerieften Klauen. Festschrift zum 60. Geburtstage von Professor Dr. Embrik Strand, Vol. I, Riga, 17 X 1936: 251–261.
- Spaeth F (1937a) Mitteilungen über Cassidinen mit besonderer Berücksichtigung der Sammlung des Naturkundemuseums der Stadt Stettin (Col.). Stettiner Entomologische Zeitung 98: 79–95.
- Spaeth F (1937b) Neue Cassidinen des Rijksmuseums in Leiden und meiner Sammlung. Temminckia 2: 135–158.
- Spaeth F (1940) Neue Cassidinen aus dem Flubgebiet des Amazonas gesammelt von S. und I. Waehner. Arbeiten über morphologische und taxonomische Entomologie 7: 141–143.

- Staines C (2002) The New World tribes and genera of hispines (Coleoptera: Chrysomelidae: Cassidinae). *Proceedings of the Entomological Society of Washington* 104: 721–784.
- Sturm J in Thon T (1828) *Abbildungen ausländischer Insecten*. 4. Coleopt. Jena, 1826–1828, 4 pp + 6 pl.
- Wagener B (1877) Cassididae. *Mitteilungen des Münchener Entomologischen Vereins* 1: 49–79.
- Wagener B (1881) Cassididae. *Mitteilungen des Münchener Entomologischen Vereins* 5: 17–85.
- Windsor DM, Riley EG, Stockwell HP (1992) An introduction to the biology and systematics of Panamanian Tortoise Beetles (Coleoptera: Chrysomelidae: Cassidinae). In: Quintero D, Aiello A. *Insects of Panama and Mesoamerica, Selected studies*. Oxford Univ. Press, Oxford, New York, Tokyo, 372–391.

A new subspecies and a new synonym of the genus *Coladenia* (Hesperiidae, Pyrginae) from China

Guo-Xi Xue¹, Yutaka Inayoshi², Hua-Lin Hu³, Meng Li¹, Ying-Dang Ren⁴

1 School of Food and Bioengineering, Zhengzhou University of Light Industry, No. 5 Dongfeng Road, Zhengzhou, Henan, 450002, China **2** Sritana Condominium 2, 96/173, Huay Kaew Rd., T. Suthep, A. Muang, Chiang Mai, 50200, Thailand **3** Jiulianshan National Nature Reserve, Longnan, Ganzhou, Jiangxi Province 341000, China **4** Institution of Plant Protection, Henan Academy of Agricultural Sciences, No. 116 Huayuan Road, Zhengzhou, Henan, 450002, China

Corresponding author: Guo-Xi Xue (xueguoxi95227@163.com)

Academic editor: Carlos Peña | Received 19 May 2015 | Accepted 11 August 2015 | Published 25 August 2015

<http://zoobank.org/1D595664-4AB4-4FFC-A0BD-BE3853EC887C>

Citation: Xue G-X, Inayoshi Y, Hu H-L, Li M, Ren Y-D (2015) A new subspecies and a new synonym of the genus *Coladenia* (Hesperiidae, Pyrginae) from China. ZooKeys 518: 129–138. doi: 10.3897/zookeys.518.10011

Abstract

The second subspecies of *Coladenia buchananii* (de Nicéville, 1889), viz. *Coladenia buchananii separafasciata* Xue, Inayoshi & Hu, **ssp. n.**, is discovered from south Jiangxi Province and west Fujian Province, southeast China. External and genital characters of both male and female of this new subspecies are illustrated and described. *Coladenia neomaeniata* Fan & Wang, 2006, **syn. n.** is proposed to be a junior synonym of *C. maeniata* Oberthür, 1896, and the distribution of this species is briefly discussed.

Keywords

Taxonomy, wing pattern, genitalia, fauna, distribution, *Coladenia buchananii separafasciata*, *Coladenia neomaeniata*, *Coladenia maeniata*

Introduction

Coladenia buchananii (de Nicéville, 1889) was described based upon a single female collected in north Myanmar. It is distributed in Myanmar (Evans 1949), Thailand (Ek-Amnuay 2006) and Laos (Osada et al. 1999), and was recorded for the first time from northwest Yunnan of China by Huang (2003) with a brief note on its habit.

During our study of the butterfly fauna in Jiulianshan National Nature Reserve, south Jiangxi Province, we captured two male skippers, which possess male genitalia nearly identical to those of *Coladenia buchananii*, but their wing patterns are conspicuously different from the latter. Considering the geographic gap between south Jiangxi and the range of *C. buchananii*, we believe that the two specimens represent a new subspecies of *C. buchananii*. Additionally, while sorting the butterfly collection in the Institute of Zoology, Chinese Academy of Sciences, the first author found a female specimen collected from west Fujian Province more than 20 years ago, and it bears almost the same wing markings as the two males from south Jiangxi. Since both sexes of all the known species in the genus *Coladenia* always have similar appearance, this female should undoubtedly belong to the new subspecies from Jiangxi. Thus, we describe this new subspecies in the present paper.

Besides, *Coladenia neomaeniata* Fan & Wang, 2006 is treated as a junior synonym of *C. maeniata* Oberthür, 1896, because they have identical male genitalia, and according to the existing distributional data, their external differences do not show a subspecific division and can only be considered as intraspecific individual variation. The range of this species is clarified based on information from literature and specimens.

Materials and methods

The following specimens of *Coladenia buchananii buchananii* (de Nicéville, 1889) were examined and compared with the new subspecies: Thailand: 1 male, Chiang Mai, Doi Suthep, 4 April 1983; 2 males, *ditto*, 3 April 1987; 2 males, *ditto*, 7 April 1987; 1 male, *ditto*, 16 March 1988; 2 males, *ditto*, 12 April 1988; 1 male, *ditto*, 26 March 1992; 1 male, Tak, Umphang, Ya Mo Kwi, 17 March 1994; 1 male, Lampang, Mae Pam, 10 April 2014. All these specimens are in the private collection of the junior author of the present paper.

Specimens of *Coladenia maeniata* Oberthür, 1896 listed as follows were examined and compared with *Coladenia neomaeniata* Fan & Wang, 2006. China: Yunnan: 3 males, Gongshan, Bingzhongluo, 16 May 2011; 3 males, Deqin, 3000 m, 18 June 2014. All these specimens were collected by Mr. Chun-Hao Wang, Beijing, and are preserved in his private collection.

The Comstock-Needham venation system was used in this paper. The terminology of genitalia mainly follows that of Shirôzu (1960).

The holotype and the male paratype of the new subspecies are deposited in School of Food and Bioengineering, Zhengzhou University of Light Industry. The female paratype is kept in the Institute of Zoology (IOZ), Chinese Academy of Sciences.

Results

Coladenia buchananii separafasciata Xue, Inayoshi & Hu, ssp. n.

<http://zoobank.org/ECE754E0-3281-4EB4-8DC8-CC9961556F4D>

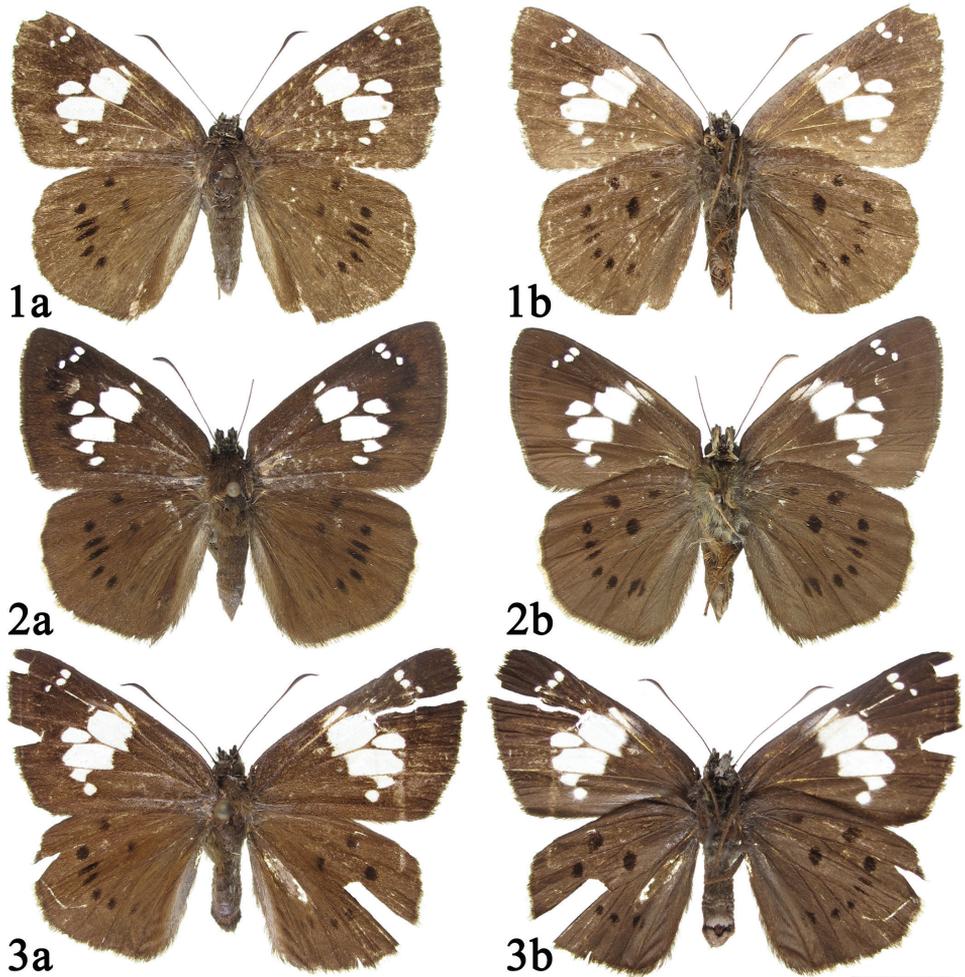
Figs 1–3, 4, 5–12, 13

Description. Male. (Figs 1–2, 4) Antennae: 12.5 mm in length, dorsal side shaft dark brown and club black, ventral side basal half dark brown and distal half covered with milky white scales, apiculus slender and sharply pointed. Labial palpi: second segment covered with white scales and black hairs, mixed with some black scales; third segment correct, with a blunt point, much thicker than the shaft of antennae, dorsal side black, ventral side with white and black scales. Thorax and abdomen: dark brown, hind tibiae with a pale yellowish hair pencil. Forewing: 22.5 mm in length, dorsal side dark brown, spots white; apical spot in space r_4 closer to the one in r_3 than to that in r_5 ; strip in space sc shorter than half length of widest portion of cell spot; cell spot big, rectangular, inner edge straight and outer upper angle concave; spot in space cu_1 narrower and longer than cell spot, its outer lower angle protrudent, overlapping with cuniform spot in space m_3 ; under spot in space cu_1 there are two separated spots in space cu_2 , of which the lower one moved inwards; all apical and discal spots are accompanied by dark shadows. Ventral side of forewing, white spots repeat those on above, except there is a white strip in space c before the one in sc. Hindwing dark brown dorsally, basal area covered with hairs; discal area with a series of black spots from space $sc+r_1$ to cu_2 , of which the two in spaces m_1 – m_2 longer and looked like an equal sign, and the two in cu_2 blurred; cell with an obscure black spot. Ventral side, all spots in discal series clearly present, base of space $sc+r_1$ with black spot, cell spot distinct and bigger than all other spots. Cilia on forewing dark brown, mixed with milky white at end of the upper half of space cu_2 ; cilia on hindwing milky white.

Male genitalia (Figs 5–12). Tegumen produced forwards and dorsally humpy in lateral view. Uncus beak-like with a sharp point in lateral view, tapered and elongated to a short finger-like blunt tip in dorsal view; its base with an auriform process on each side. Gnathos arm-like in lateral view, connected on ventral side, its tip with tiny teeth. The upper half of the ring straight, and the lower half curved. Saccus very short. Valva broad, trapezoidal, with its distal portion widely bifid into two branches, of which the upper one short and curved downwards, decorated with small teeth, the lower one elongated and curved upwards, its tip with tiny teeth. Aedeagus a little shorter than ventral margin of valva; in lateral view, coecum penis slender and curved upwards, with a rounded head; subzonal sheath shorter than suprazonal sheath; left side of the middle of suprazonal sheath bear a leaflike sheet, its edge with sawteeth. Juxta cordiform.

Female (Fig. 3). Similar to male. Forewing 22.5 mm in length, strip in space sc longer than half length of widest portion of cell spot; end of abdomen with dense gray hairs.

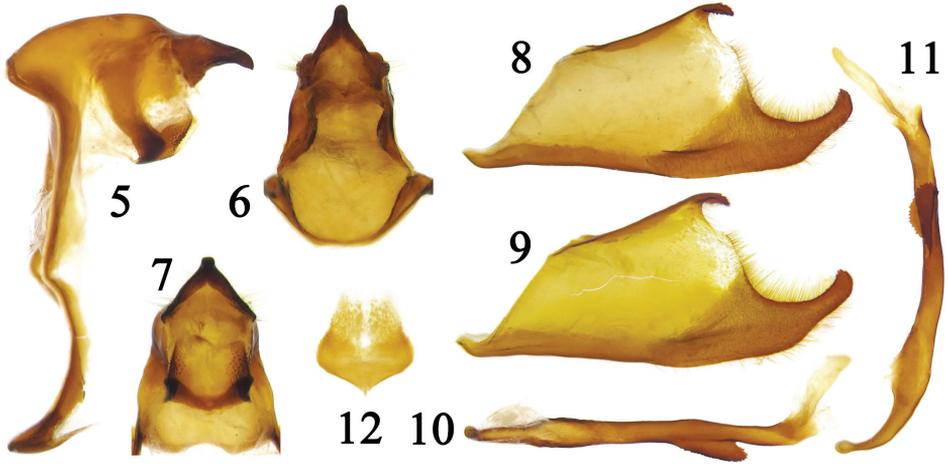
Female genitalia (Fig. 13). Papillae anales reniform, covered with short hairs. Apophyses posteriors a little longer than papillae anales. Lamella postvaginalis wide, with



Figures 1–3. Adults of *Coladenia buchananii separafasciata* Xue, Inayoshi & Hu, ssp. n. 1–2 male 3 female **a** dorsal side **b** ventral side. Scale bar: 1 cm.



Figure 4. Male adult of *Coladenia buchananii separafasciata* Xue, Inayoshi & Hu, ssp. n. in the nature. Photo by Hua-Lin Hu at the type locality, 17 April 2013.



Figures 5–12. Male genitalia of *Coladenia buchananii separafasciata* Xue, Inayoshi & Hu, ssp. n. **5** ring, lateral view **6** uncus, dorsal view **7** gnathos, ventral view **8** right valva, inner view **9** left valva, outer view **10** aedeagus, dorsal view **11** aedeagus, lateral view **12** juxta.



Figure 13. Female genitalia of *Coladenia buchananii separafasciata* Xue, Inayoshi & Hu, ssp. n., ventral view, with a close-up view of the apophyses posteriors.

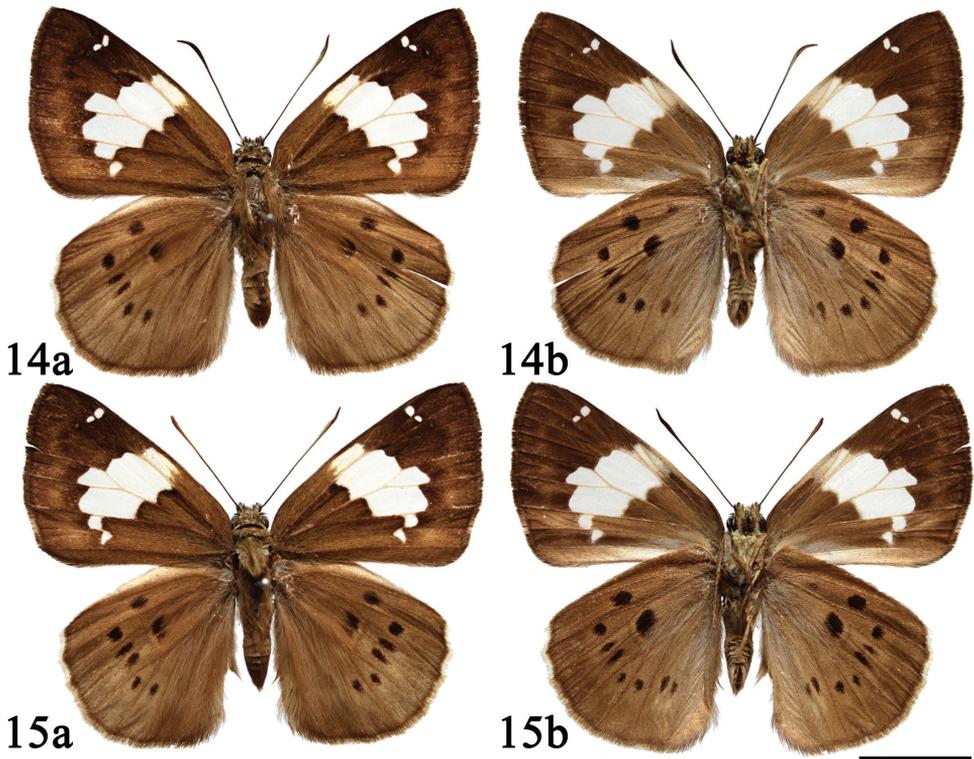
flat edge. The middle of the edge of lamella antevaginalis widely V-shaped. Sternum of seventh segment of abdomen sclerotized into a solid plate, with its posterior edge shallowly coved. Ductus bursae and bursa copulatrix bursiform, membranous, without signum.

Type material. Holotype: male, dry pinned, with genitalia preserved in glycerin. China: Jiangxi Province, Longnan County, Jiulianshan National Nature Reserve, Xiagongtang, 600 m, 7 May 2013, leg. Hua-Lin Hu. Paratypes: 1 male, *ditto*, 2 May 2013; 1 female, dry pinned, IOZ(E)1687887, with genitalia preserved in glycerin. China: Fujian Province, Jiangle County, Longqishan, Lishan, 650 m, 20 May 1991, leg. Hong-Xing Li.

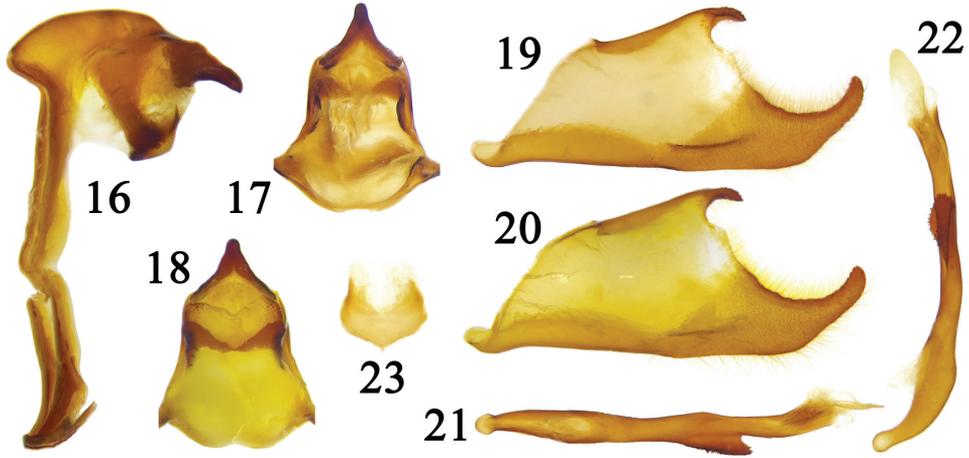
Distribution. China (S. Jiangxi, W. Fujian).

Difference with *Coladenia buchananii buchananii* (de Nicéville, 1889)

Eleven male specimens of *Coladenia buchananii buchananii* (de Nicéville, 1889) were collected from Thailand by the second author of this paper, two of them were dissected and illustrated herein (Figs 14–15, 16–23). According to these specimens and the images of female *Coladenia buchananii* in literature (de Nicéville 1889, Swinhoe 1912–1913, Ek-Amnuay 2006), the nominate subspecies is distinguishable from the new subspecies by the following combination of characters:



Figures 14–15. Male adults of *Coladenia buchananii buchananii* de Nicéville, 1889. **a** dorsal side **b** ventral side. Scale bar: 1 cm.



Figures 16–23. Male genitalia of *Coladenia buchananii buechananii* de Nicéville, 1889. **16** ring, lateral view **17** uncus, dorsal view **18** gnathos, ventral view **19** right valva, inner view **20** left valva, outer view **21** aedeagus, dorsal view **22** aedeagus, lateral view **23** juxta.

1. Ground color on both sides of the wings is paler.
2. On the dorsal side of forewing, the discal spots closely connected with each other and formed a wide band; the strips in space c and space sc combined into a wide bar, longer than half the length of the widest portion of cell spot. On the ventral side of forewing, the discal band reaches Costa.
3. Cilia on hindwing is milky white before the end of vein M_1 , and brown from the end of vein M_1 to the tornus.
4. The base of uncus in male genitalia without auriform process.
5. The coecum penis of aedeagus is thicker and shorter, not conspicuously constricted before the head.

Bionomics. Year round collecting indicates that this new subspecies is probably univoltine, only known from mid April to mid May, about one month later than the nominate subspecies which mainly appears from mid March to mid April. The two male types were captured at roadside, very near to a residential area in Jiulianshan National Nature Reserve.

Etymology. The subspecific epithet is a combination of the prefix separa- and the Latin fasciata, referring to the broken band on forewing.

Coladenia maeniata Oberthür, 1896

Coladenia maeniata Oberthür, 1896: 42, pl. 9, fig. 164 (original description). Type locality: Maenia, Thibet [sic]; Elwes and Edwards 1897: 130 (diagnosis, distribution); Swinhoe 1912–1913: 71 (distribution); Evans 1949: 118 (description,

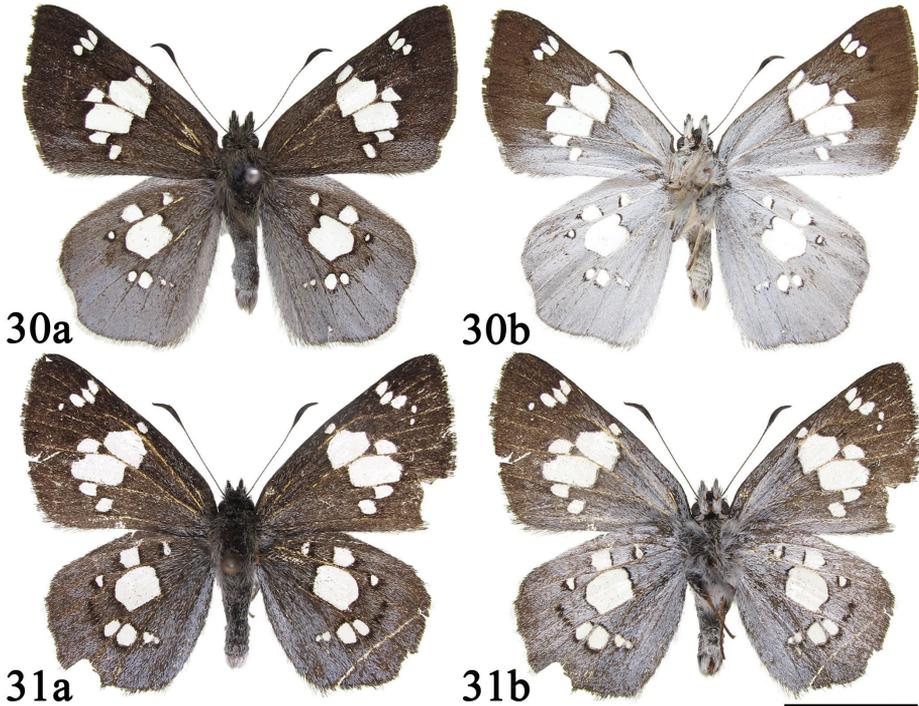
distribution); Huang 2003: 68 (distribution); Fan and Wang 2006: 79, 80 (distribution, diagnosis).

Coladenia neomaeniata Fan & Wang, 2006: 79 (original description). Type locality: Weixi County, Yunnan Province. syn. n.

Notes. According to Fan and Wang (2006), *Coladenia neomaeniata* is different from *C. maeniata* in having the valva of the male genitalia conspicuously narrowed distally, and the inner edge of the spot in space $sc+r_1$ on hindwing not in line with that of the cell spot. The first author of the present paper examined some specimens from north-west Yunnan which have the same wing pattern as *C. neomaeniata*, and found that the valva of the male genitalia is bowl-like (Figs 24, 25), and its inner side looks different depending on the angle of view (Figs 26–29): from a certain angle to see, its distal part is narrowed as shown by figure 5 in Fan and Wang (2006) (Fig 27), but from another view angle, it agrees with the figure provided by Evans (1949) (Fig 26); besides, figure 6 in Fan and Wang (2006) is the dorsal view of the valva, not later view. Thus, the male genitalia of *C. neomaeniata* is actually identical to that of *C. maeniata*. Moreover, *C. neomaeniata* is in the distributional range of *C. maeniata* (Evans 1949, Fan and Wang 2006), so their difference in the position of the spot in $sc+r_1$ on hindwing should be considered as intraspecific individual variation rather than subspecific differentiation. Such variation also appears in the shape of the spot in space sc on forewing which changes from a tiny dot to a long strip (Fan and Wang 2006, Oberthür 1896) (Fig 30), and also in the spots in spaces m_1 and m_2 which may be fully developed (Fig 31), vestigial (Oberthür 1896) or absent (Fan and Wang 2006). Therefore, *C. neomaeniata* is treated as a junior synonym of *C. maeniata* herein.



Figures 24–29. Right valva of the male genitalia of *Coladenia maeniata* Oberthür, 1896. **24** dorsal view **25** ventral view **26–29** inner side from different view angle.



Figures 30–31. Male adults of *Coladenia maeniata* Oberthür, 1896. **a** dorsal side **b** ventral side. Scale bar: 1 cm.

Remarks. Fan and Wang (2006) recorded the distribution of *C. maeniata* in south-east Xizang. We have not found any information from their work and other literature which shows this species is distributed in southeast Xizang, except that the type locality was recorded as Maenia, E. Tibet (Elwes and Edwards 1897). But the geographic range of Tibet in old entomological literature is much bigger than that of Xizang (= Tibet Autonomous Region) in nowadays. According to Elwes and Edwards (1897), Maenia is a place near Ta-t sien-lo, viz. Ta-t sien-lu, which is now known as Kangding area in west Sichuan Province, not in the range of Xizang. Then, the distribution of *C. maeniata* should be clarified as northwest Yunnan and west Sichuan (Evans 1949).

Acknowledgements

We express our sincere thanks to the following colleagues for their kind help: Dr Chun-Sheng Wu (Beijing), Mrs Hong Liu (Beijing), Mr Chun-Hao Wang (Beijing), Mr Hao Huang (Qingdao), Dr Kotaro Saito (Tokyo), Mr Xu-Guang Bai (Zhengzhou), Mrs Yu-Xiang Zhou (Zhengzhou), Mrs Lin-Lin Yang (Zhengzhou), Mr Jian-Qing Zhu (Shanghai) and Dr Song-Yun Lang (Chongqing). This study is supported by the National Natural Science Foundation of China (No. 41401067, No. 31172141).

Reference

- de Nicéville L (1889) On new and little-known butterflies from the Indian region, with a revision of the genus *Plesioneura* of Felder and of authors. Journal of the Bombay Natural History Society 4(3): 163–194.
- Ek-Amnuay P (2006) Butterflies of Thailand. Fascinating insects Vol. 2 (1st Ed). Amarin Printing and Publishing, Bangkok, 844 pp.
- Elwes HJ, Edwards J (1897) A revision of the Oriental Hesperiiidae. Transactions of the zoological Society of London 14(4): 101–324, pls. 18–27.
- Evans WH (1949) A catalogue of the Hesperiiidae from Europe, Asia and Australia in the British Museum (Natural History). The British Museum, London, 502 pp.
- Fan XL, Wang M (2006) A new species of the genus *Coladenia* Moore from China (Lepidoptera: Hesperiiidae). Journal of the Kansas Entomological Society 79(1): 78–82. doi: 10.2317/0406.23.1
- Huang H (2003) A list of butterflies collected from Nujiang (Lou Tse Kiang) and Dulongjiang, China with descriptions of new species, new subspecies and revisional notes. Neue Entomologische Nachrichten 55: 3–114.
- Oberthür C (1896) De la variation chez les lépidoptères. Études d'entomologie 20: 1–74, 13 pls.
- Osada S, Uémura Y, Uehara J (1999) An Illustrated Checklist of the Butterflies of Laos PDR. Mokuyo-sha, Tokyo, 240 pp.
- Shirôzu T (1960) Butterflies of Formosa in Color. Hoikusha Publishing Co., Ltd, Osaka, 481 pp.
- Swinhoe C (1912–1913) Vol. X. Rhopalocera: Family Hesperiiidae (concluded). In: Moore F (Ed.) Lepidoptera Indica. L. Reeve and Co., London, 1–364.

The Myriapoda and Onychophora collection (MY) of the Muséum national d'Histoire naturelle (MNHN, Paris)

Gwenaël Le Bras^{1,2}, Jean-Jacques Geoffroy³, Laurent Albenga¹, Jean-Paul Mauriès⁴

1 Muséum national d'Histoire naturelle, Direction des collections, Unité de gestion des collections Arthropodes terrestres, CP 49/50, 57 rue Cuvier, 75231, Paris Cedex 05, France **2** Muséum national d'Histoire naturelle, équipe e-ReColNat, CP 49/50, 57 rue Cuvier, 75231, Paris Cedex 05, France **3** Muséum national d'Histoire naturelle, Département Ecologie & Gestion de la Biodiversité, UMR 7204 CESCO CNRS-MNHN-UPMC, 4 avenue du Petit Château, 91800, Brunoy **4** Attaché honoraire - Muséum national d'Histoire naturelle, Département Systématique & Evolution, CP 53, 57 rue Cuvier, 75231, Paris Cedex 05, France

Corresponding author: Gwenaël Le Bras (lebras@mnhn.fr)

Academic editor: Pavel Stoev | Received 1 July 2015 | Accepted 12 August 2015 | Published 25 August 2015

<http://zoobank.org/1C69D426-4335-42C9-AD89-5D5B0A6885A7>

Citation: Le Bras G, Geoffroy J-J, Albenga L, Mauriès J-P (2015) The Myriapoda and Onychophora collection (MY) of the Muséum national d'Histoire naturelle (MNHN, Paris). ZooKeys 518: 139–153. doi: 10.3897/zookeys.518.10223

Abstract

The Myriapoda and Onychophora collection dataset inventories the occurrence records of the collection of myriapods and onychophorans in the Muséum national d'Histoire naturelle, Paris. The dataset currently consists of 202 lots of onychophorans, representing all of those present, and almost ten thousand (9 795) lots of myriapods, representing 33 to 40% of the MNHN Myriapoda collection. This collection, which is of key historic importance, represents the results of two centuries of myriapod and onychophoran studies. The sources of the collection are worldwide, with a high representation for metropolitan France for the myriapods. None of the occurrences are yet georeferenced. Access to the dataset via the data portals of the MNHN and the GBIF has been made possible through the e-ReColNat project (ANR-11-INBS-0004).

The Myriapoda and Onychophora collection of MNHN is actively expanding, hence both the collection and dataset are in continuous growth. The dataset can be accessed through the portals of GBIF at <http://www.gbif.org/dataset/3287044c-8c48-4ad6-81d4-4908071bc8db> and the MNHN at <http://science.mnhn.fr/institution/mnhn/collection/my/item/search/form>.

Keywords

Occurrence, Specimen, Myriapoda, Chilopoda, Diplopoda, Pauropoda, Symphyla, Onychophora, Taxonomy, Specimens, Collections, Types

Description

Established in the second half of the 19th century, the MNHN's combined collection of myriapods and onychophorans is still treated as one unit, mostly for historical and practical reasons.

The myriapod collection is a major resource for various studies on the group worldwide. The material comes from all around the world and represents the classes Paupoda (2 extant orders), Symphyla, Chilopoda (5 extant orders) and Diplopoda (16 extant orders), collected from most terrestrial ecosystems. About 5 000 species of myriapods are represented in the collection, including a high number of historic samples. The myriapod collection comprises between 300 000 and 400 000 specimens. Nearly half of it constitutes the identified reference collection, the other half, which includes a potentially important number of taxa yet unknown to science, is awaiting study. The identified reference collection comprises between 25 000 and 30 000 lots, each containing from 1 to more than 300 specimens, stored in 4 639 jars. The identified reference collection includes between 3 000 and 3 500 lots, containing altogether 15 000 to 20 000 type specimens.

To date, the MNHN-MY dataset covers 9 795 lots of myriapods, consisting of 63 617 specimens, which represents between 33% and 40% of the reference collection.

The MNHN collection of onychophorans (commonly known as velvet worms) is one of the world's most important for this group, including invaluable historical material, such as type specimens of species described by Louis Eugène Bouvier (1856–1944) in the early 1900s. Although only a small phylum, it is of key importance in several respects within the Metazoa, particularly regarding phylogenetic relationships between arthropods and other invertebrates (Oliveira et al. 2012). The collection boasts almost a hundred species, represented by 202 lots containing 279 specimens and 43 dissections. It is stored in 67 jars. The type material represents 56 lots containing 73 type specimens (plus 2 dissections of types).

This part of the collection is fully incorporated in the MNHN-MY dataset, which has since been used for studies on the group (Oliveira et al. 2012).

History of the collection

Myriapods: The real creation of a myriapod collection dates back to the combining of the type specimens of Paul Gervais (1816–1879) and Pierre Hippolyte Lucas (1814–1899) in the 19th century. From 1890 to 1935, this collection was enriched by the donation of the material studied by Henry Wilfred Brolemann (1860–1933) [after World War I, Brolemann modified his legal name from Brölemann to Brolemann; hereafter we use the latter spelling]. This collection contains a very large number of samples, including many type specimens of taxa described by Brolemann himself, but also by many of the most famous myriapodologists of his time (e.g. Attems 1908). Thus the collection was enriched with material from metropolitan France related to

Brolemann's prolific work on the myriapod fauna of this sector, gathered by himself and by various collectors, institutes and programmes, such as Biospeleogica (Brolemann 1923, 1930, 1935, Duboscq et al. 1933; for a complete list of Brolemann's publications, see the MyriaLit Database <http://www.myriapodology.org/myrlit/>). The collection was also enriched by samples collected during his many travels before he joined the MNHN (he lived in the United States of America and in Italy) (Duboscq 1933). Also, as a world authority on the group, Brolemann received material from all over the world for study (Brolemann 1896a, 1896b, 1897, 1898, 1909, 1920, 1922, 1926, MyriaLit Database). The MNHN collection had become a major centre for myriapodology attracting numerous international specialists who studied the collection and donate new material to the collection, such as Reginald Innes Pocock (1863–1947), Filippo Silvestri (1873–1949), Ralph Vary Chamberlin (1879–1967), Karl Wilhelm Verhoeff (1867–1945), Carl Attems (1868–1952), Otto Schubart (1900–1962) and Karl Kraepelin (1848–1915) (Kraepelin 1910a, 1910b). In addition, the collection received specimens from correspondents of the MNHN, such as Henri Gadeau de Kerville (1858–1940) (Anonymous 1941).

After 1940, the collections were enriched by donations to the Muséum national d'Histoire naturelle. The important collection built up by Paul Remy (1894–1962), who in particular studied the speleological fauna of Europe, the Balkans, northern America and northern Africa, greatly increased the MNHN-MY holdings of pauropods, a group that he studied extensively, as well as those of symphylans (Condé 1962, 1963). During the same period, the collection was enriched by the study collections of former students and collaborators of Brolemann, such as Jules Chalande (1854–1930) and Henri Ribaut (1872–1967) (Ribaut 1922). The subsequent growth and curation of the collection was the result of the work of Jean-Marie Demange, Jean-Paul Mauriès, Monique Nguyen Duy-Jacquemin and today Jean-Jacques Geoffroy and international specialists, such as Sergei Golovatch.

The collection continues to grow at a rate varying from several dozens to several thousands of specimens every year. Among the recent acquisitions, the most valuable for science are those from Madagascar, French Guiana, Brazil, different European ecosystems (high mountains, deep caves, transformed forests), China and south-east Asia, especially the material from the 2005 and 2006 expeditions to Clipperton Island and Santo (Vanuatu).

Onychophorans: The creation of the MNHN collection of onychophorans is closely linked with the interest that Bouvier developed for this group. Alongside his numerous interests and studies on crustaceans, pycnogonids, cetaceans and molluscs, Bouvier, was Director of Entomology at the MNHN from 1895 to 1931, and a pioneering researcher on onychophorans (Caulery 1944). He managed to obtain samples through institutional exchanges and described many new taxa from all over the distribution areas of the two extant onychophoran families (South America, southern Africa and Australasia). Based on this collection, Bouvier built his monograph of the onychophorans, which is a milestone for the scientific knowledge on this group (Bouvier 1905, 1907b). In 1907, when he published a catalogue of the collection, it already

boasted 92 lots, containing 38 species plus about 6 varieties (Bouvier 1907a). Since Bouvier's death in 1944, the collection has grown at a much slower rate.

In 2000, this collection was completely revised by one of the major specialists of this group, Hilke Ruhberg (University of Hamburg, Germany).

Project details

Project title: Digitization and provision of the data from the Muséum national d'Histoire naturelle to the international community.

Personnel: Gwenaël Le Bras (data publisher, data manager), Jean-Jacques Geofroy (curator, data manager, collection identifier, data collector), Laurent Albenga (data publisher, data manager), Jean-Paul Mauriès (data collector, collection identifier, data publisher, data manager, former curator).

Funding: e-ReColNat : ANR-11-INBS-0004, Muséum national d'Histoire naturelle, Paris (MNHN).

Study area descriptions/descriptor: The dataset corresponds to those parts of the collection of myriapods and onychophorans of the MNHN that have already been entered into the database. The present dataset does not represent the totality of the collection, since its digitization is still incomplete. This collection is an invaluable legacy for knowledge of myriapods and onychophorans, in terms of its history, size and high proportion of type specimens. Uploading this dataset to shared database systems was therefore important for the future uses of the collection, to provide easy access by researchers and the general public to the detailed data it contains. This also provides better conservation of the data, because shared systems are better lasting solutions than local computers. The main goal of the e-ReColNat project in this case was to refine and transfer the existing metadata from a local, mono-table database (4D system) to the MNHN's shared collection database system (Oracle), and to allow its publishing through the MNHN web services and the GBIF portal. One entry corresponds to a lot, consisting of one to several specimens sharing the same collection data and belonging to the same taxon.

Design description: From the mid-1980s, the collection curators and researchers J.-P. Mauriès and J.-M. Demange have been digitizing the data, mostly in relation to their taxonomic work, on a local database (4D). By 2010, the database had reached ca. 10 000 entries. This database was originally created simply to be requested only by jar or lot identifier. Therefore, this large dataset needed both structuring and refining in order to allow multi-field requests before being integrated into the MNHN shared collection database system (Oracle) and connected to the GBIF infrastructure through an Integrated Publishing Toolkit (IPT) (Soberón et al. 2002). Initial work was conducted in 2011 by Laurent Albenga to upload all 202 entries for onychophorans. The remaining 9 795 myriapod entries have been refined in the scope of the e-ReColNat project by Gwenaël Le Bras, and were committed to the MNHN shared collection database system on 27th January 2015, being harvested by GBIF on 16th March 2015. In addition to Oracle solutions and to the MNHN's in-house JACIM systems for sci-

entific management (http://collections.mnhn.fr/wiki/Wiki.jsp?page=Jacim_Documentation), OpenRefine (<http://www.openrefine.org>) proved to be a very precious tool in the refining process. Geographical analyses of the dataset, including the maps presented here, were made using Quantum GIS mapping software (<http://www.qgis.org>) and the Thematicmapping.org world borders dataset (http://thematicmapping.org/downloads/world_borders.php). The databasing is carried out at the lot level, with information concerning identification, nomenclatural status, number of specimens, sex and development state, geographical origin, type of collection, collecting method. The geographical coverage of the dataset reflects the activities of scientist's with these collections during the past decades. The portions of the collection that have been recently studied tend to be more scattered (fewer specimens per lot and fewer lots per jar).

Data published through GBIF: <http://collections.mnhn.fr/ipt/resource.do?r=mnhn-my>

Taxonomic coverage

General taxonomic coverage description: As depicted in Figures 1 and 2, to the exception of the onychophorans, the dataset reflects the scientific activities of the researchers carrying out the digitization. Consequently, even though the collection taxonomically covers all myriapods and onychophorans, the dataset mostly comprises millipedes. The digitization work was conducted together with a revision of the specimens concerned, and often leads to a splitting of the original lots into smaller ones. As a result of this, these two collections are also more scattered than the others, with less specimens per lot, as depicted in Figure 3. The taxonomy used in the dataset follows that used in the

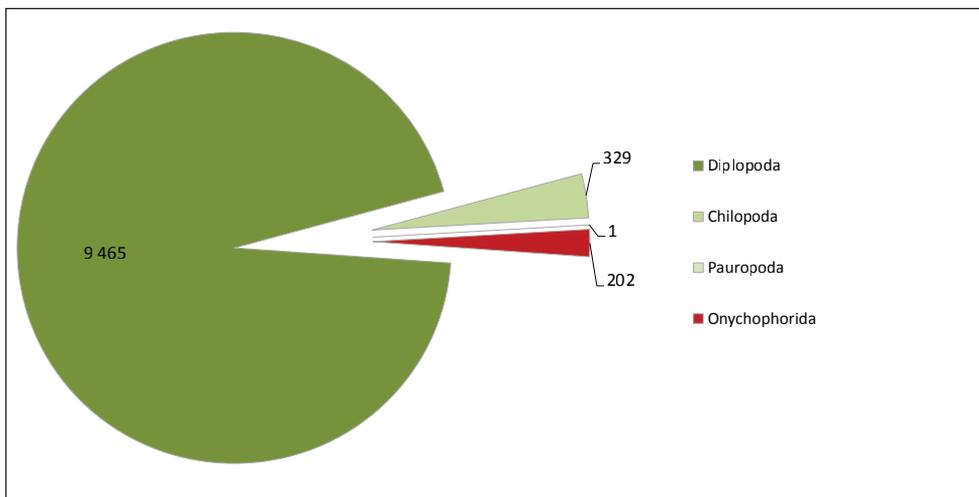


Figure 1. Taxonomic coverage (by class) of the MNHN-MY dataset in terms of number of lots. (Entries up to 27.01.2015)

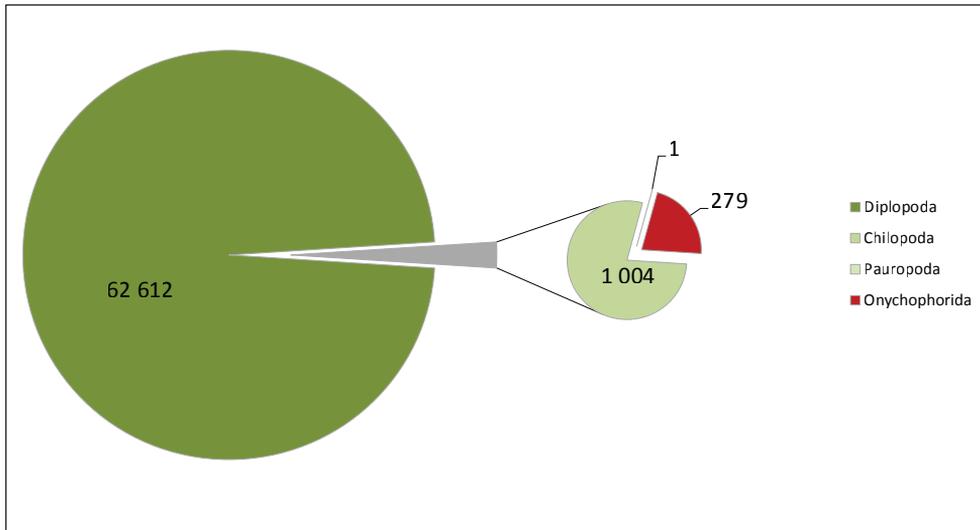


Figure 2. Taxonomic coverage (by class) of the MNHN-MY dataset in terms of number of specimens. (Entries up to 27.01.2015)

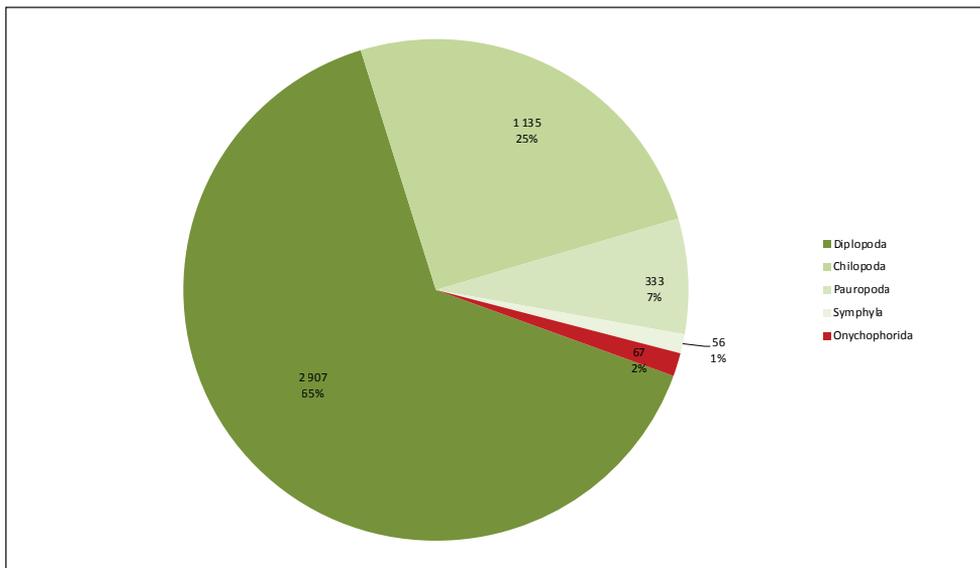


Figure 3. Taxonomic coverage (by classes) MNHN-MY reference collection in terms of number of jars.

collection. Like that of most of the large historical collections around the world, it is in many ways outdated, and would be very difficult to update in practice (Soberón et al. 2002, Gaston and May 1992, Alroy 2002).

The onychophoran collection contains 48 species and 7 subspecies, belonging to 15 genera of the two currently known extant families.

Taxonomic ranks

Kingdom: Animalia (animals)

Phylum: Arthropoda (arthropods)

Class: Chilopoda (centipedes)

Order: Geophilomorpha, Lithobiomorpha, Scolopendromorpha, Scutigermorpha

Class: Diplopoda (millipedes)

Order: Callipodida, Chordeumatida, Glomerida, Glomeridesmida, Julida, Platydesmida, Polydesmida, Polyxenida, Polyzoniida, Siphonophorida, Sphaerotheriida, Spirobolida, Spirostreptida, Stemmiulida

Class: Pauropoda

Order: Tetramerocerata

Class: Symphyla

Phylum: Onychophora (velvet worms)

Class: Onychophorida

Order: Euonychophora

Spatial coverage

General spatial coverage: No lots from this dataset have been georeferenced, but contemporary country names have been included when possible, according to ISO 3166 (http://www.iso.org/iso/country_codes.htm). The two main parts of the collection have a different spatial repartition, due in part to the distribution of the taxa represented, but also to a different history.

Myriapods: The myriapod dataset is a collection for “metropolitan France and the world”. In fact, 56.80% of the databased lots were collected in metropolitan France, representing 72.64% of the total number of specimens in the collection. This is due to the fact that the number of specimens per lot collected in metropolitan France is significantly higher than the average number of specimens per lot for the rest of the world, including the French overseas territories. Even though the metropolitan France collection has been extensively studied (and consequently its lots have been split numerous times following their taxonomic revision), they are still, on average, larger than those coming from the rest of the world. The worldwide distribution, as depicted in Figure 4, is not homogeneous. Both characteristics of the dataset, as well as the taxonomic coverage (see above), reflect the main centres of interest of Demange’s and Mauriès’ research work. The influence of Brolemann’s studies on the faunas of Algeria, Brazil and the USA (Brolemann 1896b, 1897, 1909, 1931, MyriaLit <http://www.myriapodology.org/myrlit/>) is clearly visible in Figure 5.

It is, however, highly probable that the number of specimens from metropolitan France is over-represented in the dataset, compared to the whole collection. The same phenomenon is observed when interpreting the average number of specimen per lot, as depicted on Figure 6. With the exception of a few countries, the average number

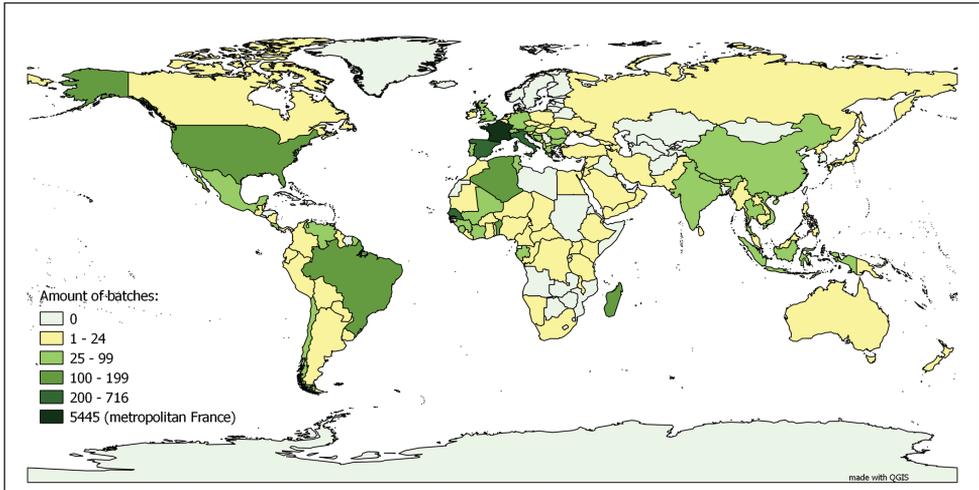


Figure 4. Origins of the myriapod lots in the MNHN-MY dataset. Based on the 9 587 lots bearing information on country of origin, out of 9 795 lots in the dataset (entries up to 27.01.2015)

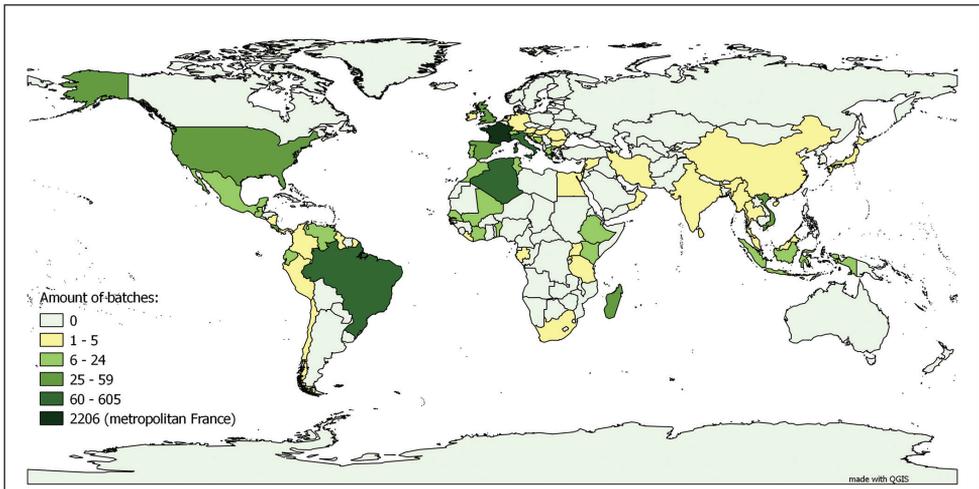


Figure 5. Origins of the myriapod lots collected prior to 1933 in the MNHN-MY dataset. Based on the 3 548 lots bearing information on country of origin, out of 3 559 lots collected before 1933 in the dataset (entries up to 27.01.2015)

of specimen per lot is relatively low (average of 4.049 specimens per lot for the non-French specimens). Also, in the distribution of the type lots, France tends to be still over-represented in the dataset, though less markedly so (see Figure 7). This due to the fact that even though France is not a “hot spot” for myriapod biodiversity, it has been and still is an intensively studied area by the specialists working on the collection.

Onychophorans: The onychophorans specimens come from the whole range of the group. One might be surprised to note in Figure 8 the importance of South Africa as a

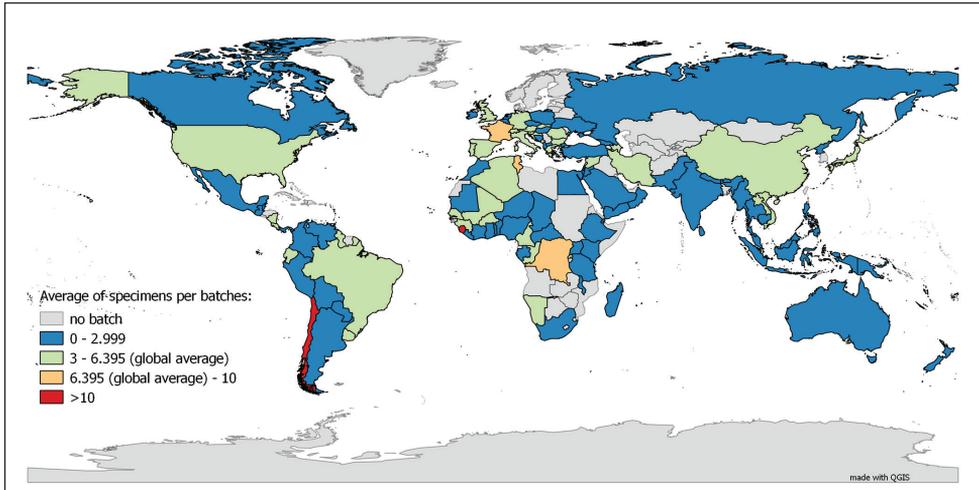


Figure 6. Average number of specimens per lot in the MNHN-MY dataset. (Entries up to 27.01.2015)

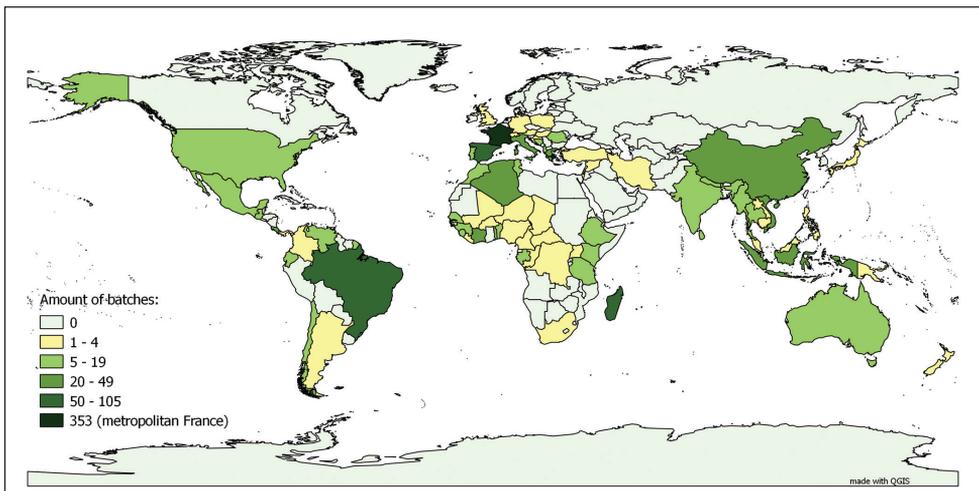


Figure 7. Origins of the myriapod lots containing type specimens in the MNHN-MY dataset. Based on the 1 137 lots of type specimens bearing information on country of origin, out of 1 170 lots containing types in the dataset (entries up to 27.01.2015)

source of specimens in the collection. These specimens were mainly obtained through exchanges made between the MNHN and other institutes, such as the British Museum (Natural History). The distribution of type material in Figure 9 largely reflects the extensive descriptive work of Bouvier on this group.

Temporal coverage: 1833 – 2010.

Myriapods: The oldest myriapod specimen databased to date is MY4389, *Rhinocricus olivaceus* (Newport, 1844), which was collected in 1835 from Mexico. How-

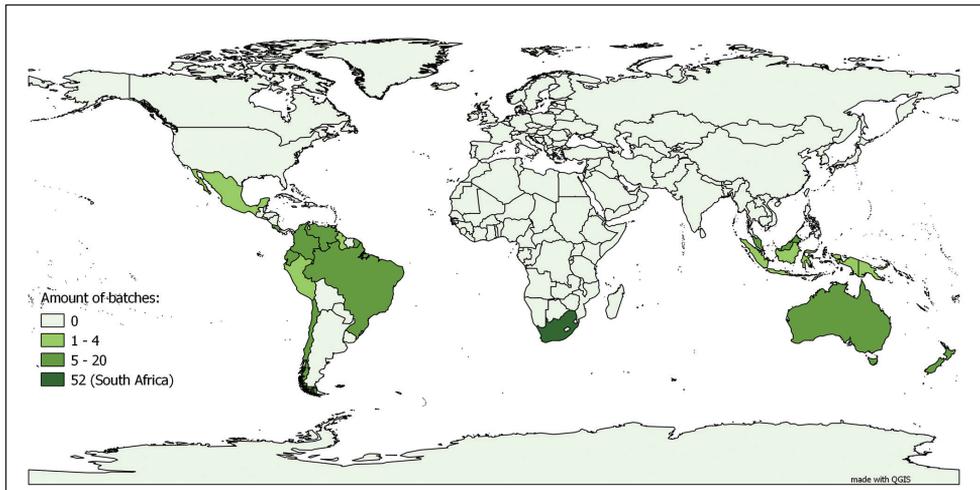


Figure 8. Origins of the onychophoran lots in the MNHN-MY dataset. Based on the 191 lots bearing information on country of origin, out of 202 lots in the dataset (entries up to 27.01.2015)

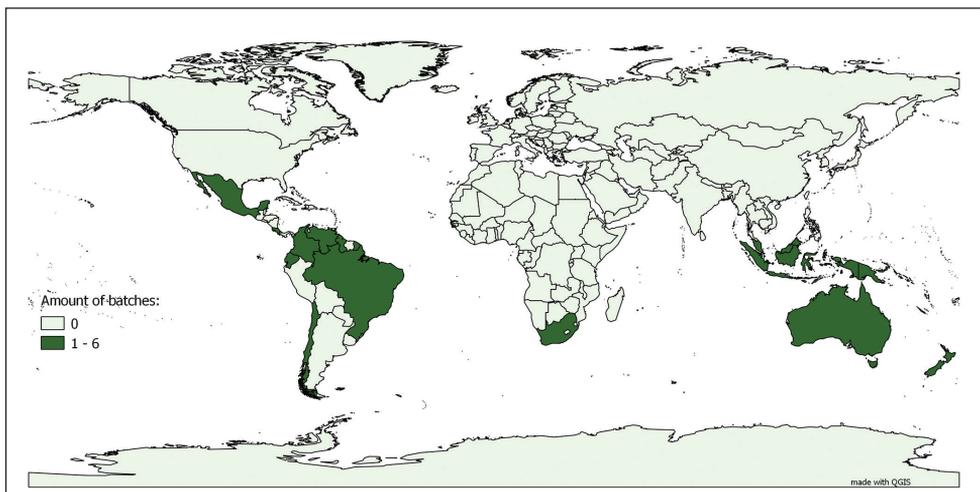


Figure 9. Origins of the onychophoran lots containing types in the MNHN-MY dataset. Based on the 56 lots of type specimens in the dataset, all of which bear information on country of origin (entries up to 27.01.2015)

ever, the acquisition rates were highest during two distinct periods, as can be seen in Figure 10. The first period corresponds to the activity of Brolemann from 1890 until his death in 1933. The second period, after World War II, corresponds to a renewal of interest in myriapodology at the MNHN, with the arrival of scientists such as Demange in 1942 and Mauriès in 1959. It should be noted, however, that specimens collected since 1990 are less well represented in the database than the older specimens, be-

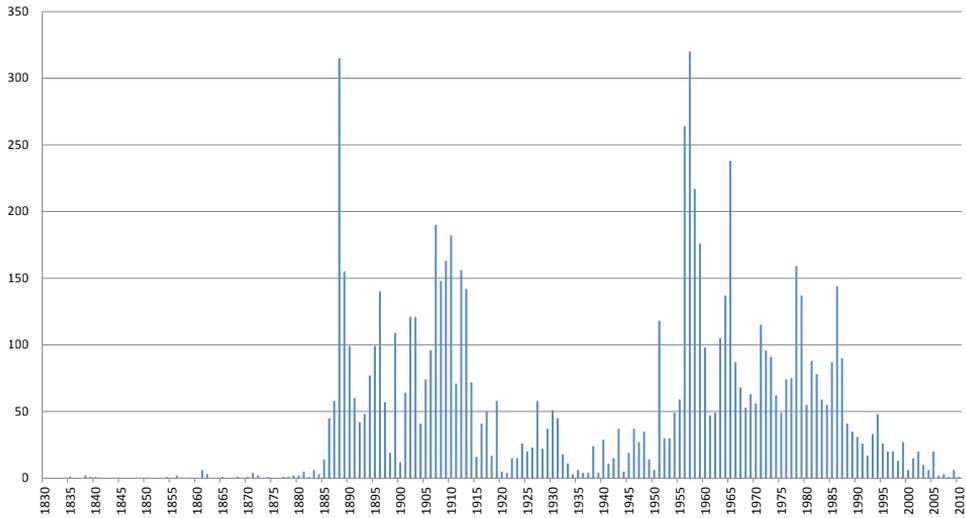


Figure 10. Number of myriapod lots by year of collection. Based on the 8 055 lots with collection date.

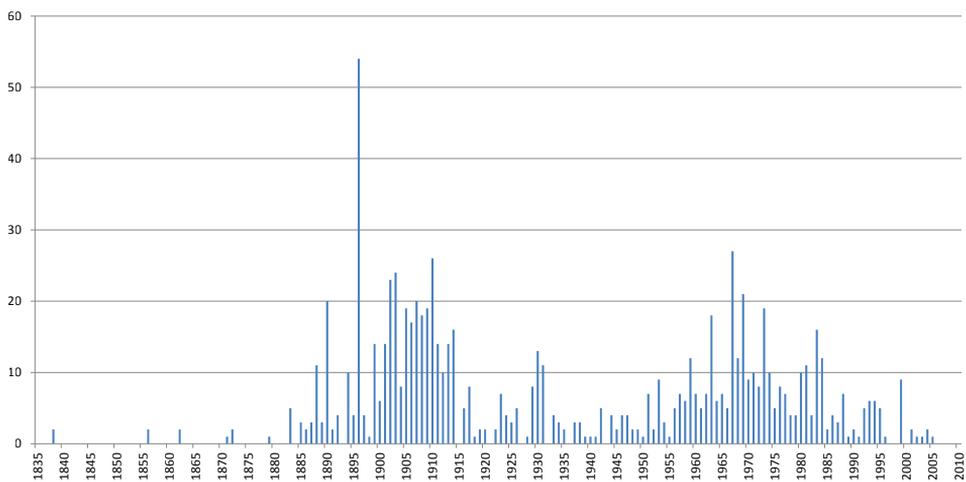


Figure 11. Number of myriapod lots containing type specimens by year of collection. Based on the 875 lots containing types with collection date.

cause they are still under study and will be progressively databased in the future. This is also illustrated in Figure 11. The number of type specimens per lot is higher during the first period than during Brolemann's activity, mainly due to his intense collecting and important taxonomic work, including the description of a large number of new taxa.

Onychophorans: The oldest onychophoran specimen, is MY110 (formerly ON111), a type specimen of *Peripatus edwardsi* Blanchard, 1847, collected in 1833 from French Guyana. However, as can be seen in Figure 12, the major part of the col-

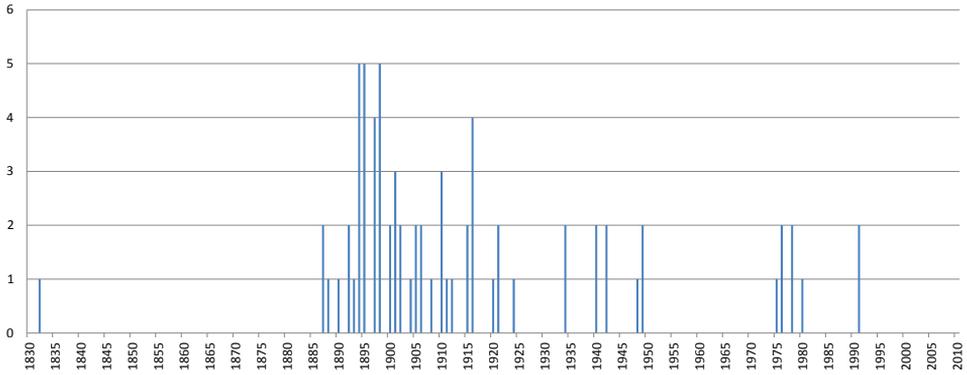


Figure 12. Number of onychophoran lots by year of collection. Based on the 72 lots with collection date.

lecting effort was carried out during Bouvier's period of activity, from 1887 to 1931. Although Bouvier described a relatively large number of onychophoran taxa, of which many types are stored in this collection, only a few of these type specimens have a collection date.

Natural collections description

Parent collection identifier: MNHN

Collection name: Myriapoda and Onychophora collection (MY) of the Muséum national d'Histoire naturelle (MNHN – Paris)

Collection identifier: MY

Formation period: 1985–2015

Methods

Specimen preservation method: Alcohol and microscope slides

Methods: The specimens are gathered into lots, each consisting of one taxon from a single sampling event. The lots are mostly preserved in 75% alcohol in tubes plugged with cotton wool and placed in jars. Out of the databased collection, about 2% of the lots are in jars, rather than tubes, mainly due to their size. Over 97% of the jars contain one tube, 0.8% contain 2–5 tubes and less than 0.2% contain more than 5 tubes. These tubes are stored in glass jars filled with alcohol to avoid evaporation inside the tubes. In addition, preparations on microscope slides are also conserved, particularly for small specimens and dissected gonopods. Each databased lot receives an inventory number prefixed by the collection acronym (MY).

Study extent description: The collection is mainly used for studies on the systematics of myriapods and onychophorans. In terms of its size, composition and number

of type specimens, it is a major resource for specialists of these taxa. Moreover, it has revealed an important number of unexpected new taxa within its previously less studied parts. The material from France and the Mediterranean areas, particularly Spain, have been extensively studied.

Sampling description: No single sampling protocol can be distinguished. Moreover, for most of the specimens, the sampling methodology is unknown, even if suspected to be by direct hand collecting in most cases.

Datasets

Dataset description

Object name: Darwin Core Archive Myriapoda and Onychophora collection (MY) of the Muséum national d'Histoire naturelle (MNHN – Paris).

Character encoding: UTF-8.

Format name: Darwin Core Archive format.

Format version: 1.0.

Distribution: <http://collections.mnhn.fr/ipt/archive.do?r=mnhn-my> and <http://science.mnhn.fr/institution/mnhn/collection/my/item/search/form>

Publication date of data: 24-03-2015.

Language: French.

Metadata language: English.

Date of metadata creation: 27-06-2014.

Hierarchy level: Dataset.

Acknowledgements

We wish to thank the ANR-11-INBS-0004 for financing the greater part of the transfer from the 4D database to the MNHN Oracle system through the ReColNAt project, Peter Decker and another, anonymous, reviewer who helped significantly to improve the manuscript, Simon Chagnoux and Bérenger Dulac (Direction des Services Informatiques, MNHN) for active collaboration on data uploading and maintenance; the GBIF-France staff, especially Sophie Pamerlon, Marie-Elise Lecoq and Anne-Sophie Archambeau, for advice on all aspects of the process from refining the data to publishing this paper. Our thanks also go to Ehoarn Bidault for critical reading of the manuscript, Elise-Anne Leguin and Christophe Hervé for help with the literature and collections, Greg Beuthin for English corrections, and particularly Mark Judson for his critical readings and English language corrections. We are grateful to all the scientists who have worked on the MY collection, particularly Hike Ruhberg (University of Hamburg, Germany), for her work on the Onychophora collection and her kind and rapid answers to our questions.

References

- Alroy J (2002) How many named species are valid? Proceedings of the National Academy of Sciences of the United States of America 99: 3706–3711. doi: 10.1073/pnas.062691099
- Anonymous (1941) Nécrologie: Henri Gadeau de Kerville. Bulletin de la Société préhistorique de France 38 (1): 6–7.
- Attems C (1908) Note sur les Myriopodes recueillis par M. Henri Gadeau de Kerville en Khroumirie, et description de deux espèces et d'une variété nouvelles provenant de cette région de la Tunisie. In: Gadeau de Kerville H (Ed.) Voyage zoologique en Khroumirie (Tunisie). Mai-Juin 1906. Avec quatre mémoires du comte Carl Attems, d'Ignacio Bolivar, du Dr Raphaël Blanchard et de Louis Germain, sur les Myriopodes, les Insectes Orthoptères, les Hirudinées et les Mollusques récoltés pendant ce voyage. J. B. Baillière & Fils, Paris, 103–116.
- Bouvier LE (1905) Monographie des Onychophores. Annales des Sciences Naturelles, Zoologie et Biologie Animale [9e Série] 2: 1–383.
- Bouvier LE (1907a) Catalogue des Onychophores des Collections du Muséum d'Histoire Naturelle de Paris. Bulletin du Muséum national d'Histoire naturelle 13: 518–521.
- Bouvier LE (1907b) Monographie des Onychophores. Annales des Sciences Naturelles, Zoologie et Biologie Animale [9e Série] 5: 61–318.
- Brolemann HW (1896a) Myriapodes provenant des campagnes scientifiques de l'Hirondelle et de la Princesse Alice. Bulletin de la Société Zoologique de France 21: 198–204.
- Brolemann HW (1896b) Liste des Myriapodes des Etats-Unis, et principalement de la Caroline du Nord, faisant partie des collections de M. Eugène Simon. Annales de la Société entomologique de France 65(1): 43–70.
- Brolemann HW (1897) Un mystérieux myriapode *Scolopendra bahiensis* Brandt. Bulletin de la Société Zoologique de France 22(5–6): 142–146.
- Brolemann HW (1898) Voyage de M. E. Simon au Venezuela (décembre 1887-août 1888). Myriapodes du Venezuela. Annales de la Société entomologique de France 67(1): 241–313.
- Brolemann HW (1909) Os myriapodos do Brazil. In: Catalogos da Fauna Brasileira vol. II. Museu Paulista, São Paulo, 1–94.
- Brolemann HW (1920) Myriapodes III. Diplopoda. In: Shultz A (Ed.) Voyage de Ch. Alluaud et R. Jeannel en Afrique Orientale (1911–1912). Résultats scientifiques. Librairie des Sciences Naturelles Léon Lhomme, Paris, 49–298.
- Brolemann HW (1922) Myriapods collected in Mesopotamia and N. W. Persia by W. Edgar Evans, B.Sc., late Capt. R.A.M.C. Proceedings of the Royal Physical Society of Edinburgh 42(6): 54–74.
- Brolemann HW (1923) Biospeologica XLVIII. Blaniulidae Myriapodes (Première Série). Archives de Zoologie Expérimentale et Générale 61(2): 99–453.
- Brolemann HW (1926) Myriapodes recueillis en Afrique occidentale française par M. l'administrateur en chef L. Duboscq. Archives de Zoologie Expérimentale et Générale 65(1): 1–159.
- Brolemann HW (1930) Éléments d'une faune des myriapodes de France (Chilopodes). In: Lechevalier P (Ed.) Faune de France vol. 25, Paris, 405 pp.

- Brolemann HW (1931) Myriapodes recueillis par M. le Dr H. Gauthier en Algérie. Bulletin de la Société d'Histoire naturelle de l'Afrique du Nord 22: 121–134.
- Brolemann HW (1935) Myriapodes Diplopodes (Chilognathes I). In: Lechevalier P (Ed.) Faune de France vol. 29, Paris, 369 pp.
- Caulery M (1944) Notice nécrologique sur Louis-Eugène Bouvier (1856–1944). Comptes Rendus hebdomadaires des Séances de l'Académie des sciences 218: 89–94.
- Condé B (1962) Nécrologie – Paul A. Remy. Bulletin de la Société entomologique de France 67(5–6): 93–95.
- Condé B (1963) Notice sur Paul A. Remy et son œuvre biospéléologique. Annales de Spéléologie 18: 463–471.
- Duboscq O (1933) Henry Brölemann. Bulletin de la Société Zoologique de France 58(1): 275–277.
- Duboscq O, Ribaut H (1933) Liste des publications de H.W. Brölemann. Bulletin de la Société Zoologique de France 58(1): 278–283.
- Gaston KJ, May RM (1992) Taxonomy of taxonomists. Nature 356: 281–282. doi: 10.1038/356281a0
- Kraepelin K (1910a) Catalogue des Scolopendrides des collections du Muséum d'Histoire naturelle de Paris (Collections du Muséum déterminée par M. le Professeur Karl Kraepelin, et collection H.W. Brolemann) 1re partie – Scolopodendrides en dehors du genre *Scolopendra*. Bulletin du Muséum national d'Histoire naturelle 10: 243–255.
- Kraepelin K (1910b) Catalogue des Scolopendrides des collections du Muséum d'Histoire naturelle de Paris (Collections du Muséum déterminée par M. le Professeur Karl Kraepelin, et collection H.W. Brolemann) 2e partie – genre *Scolopendra*. Bulletin du Muséum national d'Histoire naturelle 10: 316–325.
- MyriaLit Database <http://www.myriapodology.org/myrlit/> [accessed 05.12.2014]
- Oliveira IS, Read VMSL, Mayer G (2012) A world checklist of Onychophora (velvet worms), with notes on nomenclature and status of names. ZooKeys 211: 1–70. doi: 10.3897/zookeys.211.3463
- Ribaut H (1922) Myriapodes. In: Bouvier EL (Ed.) Voyage de M. le Baron Maurice de Rothschild en Éthiopie et en Afrique Orientale Anglaise (1904–1905). Imprimerie Nationale, Paris, 129–154.
- Soberón J, Arriaga L, Lara L (2002) Issues of quality control in large, mixed-origin entomological databases. In: Saarenmaa H, Nielsen ES (Eds) Towards a global biological information infrastructure, Technical report. European Environment Agency, Copenhagen 70: 15–22.
- Thematic Mapping API http://thematicmapping.org/downloads/world_borders.php [accessed 23.10.2014]

Book Review: Los invertebrados de hábitats subterráneos de Jaén

By Pérez-Fernández, T. and Pérez-Ruiz, A

Francisco Javier Peris-Felipo¹

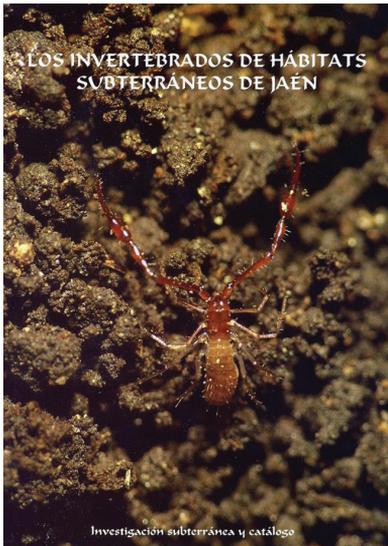
¹ Bleichstrasse 15, CH-4058, Basel (Switzerland)

Corresponding author: *Francisco Javier Peris-Felipo* (peris.felipo@gmail.com)

Received 24 March 2015 | Accepted 12 August 2015 | Published 25 August 2015

<http://zoobank.org/3E29342B-3453-4C60-9CD6-8ADAD6901934>

Citation: Peris-Felipo FJ (2015) Book Review: Los invertebrados de hábitats subterráneos de Jaén. ZooKeys 518: 155–156. doi: 10.3897/zookeys.518.9684



This book concerns the review of both the history of speleology in southern Spain and the invertebrate fauna of Jaen province within two parts: (1) ‘Historia de la Espeleología en Andalucía’; and (2) ‘Medio subterráneo y organismos hipogeos’. First contributions were carried out very early in the 20th century by Abbé Henri Breuil, Pierre-Jules Rambur, Lucas von Heyden, and Georg Dieck. However, until the late 1940s and early 1950s, no more studies were attempted. From this time, different researchers such as Joaquín Mateu, Antonio Cobos, and Dr Francesc Español, began to study the area and increase research output. During the 1970s to 1990s, many entomologists and biospeleologists belonging to different societies sampled in the Andalusian caves. At the beginning of the 21st

century, amateur societies such as ‘Grupo de Espeleología de Villacarrillo’ (G.E.V.), ‘Espeleo Club Almería’, ‘Grupo de Exploraciones Subterráneas de la Sociedad Excur-

sionista de Málaga', 'Grupo de Espeleólogos Granadinos', 'Grupo de Exploraciones Subterráneas de Priego', 'Grupo de Investigaciones Espeleológicas de Jerez' (G.I.E.X.), and 'Club Deportivo Plutón' continued exploring the caves and increasing our knowledge of hypogeal species from southern Spain.

In the second part, an explanation of the ecological subterranean landscape and the list of recorded hypogeal species from Jaen province are provided in 26 chapters. The authors list them by phylum, order, family, and species. Additionally, short descriptions of each species, its distribution, habitat, and/or some pictures are provided.

A total of 290 hypogeal species are listed including the phyla Annelida (2), Chelicerata (41), Crustacea (18), Hexapoda (148), Mollusca (16), Myriapoda (23), and Nematoda (42). These species belong to 31 orders; among them, Coleoptera is the most abundant. Also, 31 species were recorded for the first time in Andalucía: *Ablechroiulus spelaeus*, *Acipes andalusius*, *Atheta tenebrarum*, *Camaeus gevi*, *Chthonius* (*Ephippiochthonius*) *cazorlensis*, *Ch. (E.) espanyoli*, *Ch. (E.) giennensis*, *Ch. (E.) perezii*, *Ch. (E.) villacarrillo*, *Ceratosphys jabaliensis*, *Coletinia tinauti*, *Corynoptera latibula*, *Domene cavicola*, *D. perezii*, *Habrocerus ibericus*, *Laemostenus (A.) cazorlensis cazorlensis*, *L. (A.) cazorlensis divergens*, *Nemastomella gevia*, *Neobisium (Ommatoblothrus) espinoi*, *N. (O.) perezii*, *N. (O.) perezruizi*, *Nesticus baeticus*, *Petaloptila (Zapetaloptila) carabajali*, *P. (Z.) mogon*, *Protonemura gevi*, *Pseudosinella baeticaense*, *Psichrosoma baeticaense*, *Pygmarrhopalites perezii*, *Stegelletina coprohila*, *Tinautius troglophilus*, and *Trichoniscus perezii*.

To conclude the book, the authors provide information about the distribution of caves with a complete listing and map. This book is essential reading to increase and understand to the history of Andalusian speleology and, especially, to acquire knowledge of species that live in these somewhat surprising habitats.

2013, Grupo Espeleología Villacarrillo, Jaén, 188 p., Deposito Legal: J 448-2013
23.6 × 16.9 cm, colour, 13 € (\$ 14).